Historical frequency, intensity and extent of mountain pine beetle disturbance in British Columbia

René Alfaro, Elizabeth Campbell, and Brad Hawkes

Mountain Pine Beetle working paper 2009-30

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Mountain Pine Beetle Initiative PO # 2.05

Abstract

This project used dendrochronology to reconstruct the history of mountain pine beetle outbreaks over the last two centuries and to describe the relationship of outbreaks to varying climate conditions and fire history.

The history of mountain pine beetle outbreaks was reconstructed from increment cores and basal disks collected from 85 stands across British Columbia and Alberta. Using aerial survey data, dendrochronological software was calibrated to detect growth releases that could be attributed to beetle outbreaks. In addition to the outbreak in the 1970s and 1980s, growth release data indicate that beetle outbreaks probably also occurred in the late 1870s and 1900s, and in the 1930s and 1940s. Growth release periods associated with beetle outbreaks lasted up to 20 years, with the magnitude of growth increases averaging 58% to 65%. Based on time intervals between growth release periods, we estimated a return-interval of beetle outbreaks of 30 to 40 years. Although the intensity of past beetle outbreaks appears to be greater in central British Columbia than further north or in Alberta, further investigations are required. A histogram of growth release frequencies among stands suggests outbreaks have become more extensive over the last century.

Relationships between beetle outbreaks and climate variability were assessed using instrumental weather data, modelled climate data, and historical reconstructions of climate from tree-ring data. Weather station data indicated that beetle outbreaks occurred during prolonged warm periods that generated drought. Drought indices, as well as fall and spring temperatures, were reconstructed back at least 150 years using tree-ring-width data. Although drought frequency has increased at the edge of the beetles historic geographic range (e.g., Banff National Park), it has been a persistent condition in central British Columbia where outbreaks have occurred for much longer periods. Temperatures reconstructed from tree-rings showed more of an oscillating trend, but those predicted from models indicated a fairly linear increase, with spring temperatures changing most under a climate-change scenario. Drought increased similarly. As drought significantly decreases tree resistance to beetle attack and as warm spring temperatures are critical to larval survival, we expect that climate at the edges of the current beetle outbreak will continue to provide more optimal conditions for beetle outbreaks.

Relationships between the occurrence of beetle outbreaks and fire history were undertaken using several approaches in dendrochronology. Dating of fire scars in the Cariboo–Chilcotin Plateau of central British Columbia indicated that fires were much less frequent in the 20th century than they were in the 19th century. This may explain the more extensive outbreaks of the 1930s and 1940s and 1970s and 1980s in this region. Stands in regions characterized by low- or mixed-severity fire regimes had more frequent outbreaks than those in regions where fires are stand-replacing disturbance events. Among stands that originated from stand-replacing fires, we found that the time since fire had an important influence on frequency of beetle outbreaks—outbreaks were most frequent in stands 50 to 100 years after fire, when mature trees are less resistant to beetle attack and thick phloem tissues promote beetle development.

Keywords: climate change, *Dendroctonus ponderosae*, dendrochronology, forest disturbance.

Résumé

Cette étude utilise la dendrochronologie pour retracer l'historique des flambées de dendroctones du pin ponderosa au cours des 200 dernières années et pour décrire la relation qui existe entre les flambées et les changements des conditions climatiques ainsi que l'historique des feux.

L'historique des flambées de dendroctones du pin ponderosa a été recréé à partir de carottes et de plateaux issus de 85 peuplements en Colombie-Britannique et en Alberta. À partir de données tirées de relevés aériens, un logiciel pour les études dendrochronologiques a été programmé de façon à détecter les reprises de croissance qui pourraient avoir été causées par les flambées de dendroctones. En plus des flambées des années 1970 et 1980, les données sur les reprises de croissance indiquent qu'il y a sans doute eu d'autres flambées de dendroctones à la fin des années 1870 et dans les années 1900, 1930 et 1940. Les périodes de reprise de croissance associées aux flambées de dendroctones ont duré jusqu'à 20 ans, alors que les augmentations de la vitesse de croissance étaient en moyenne de 58 % à 65 %. D'après les intervalles entre les périodes de reprise de croissance, on a estimé que les flambées réapparaissaient à des intervalles de 30 à 40 ans. Bien que l'intensité des flambées de dendroctones précédentes semble être plus importante dans le centre de la Colombie-Britannique qu'au nord ou en Alberta, il faut toutefois poursuivre les études. Un histogramme affichant les fréquences de reprises de croissance indique que les flambées se sont intensifiées au cours des deux derniers siècles.

Les liens entre les flambées de dendroctones et la variabilité du climat ont été évalués à partir de données météorologiques obtenues au moyen d'instruments, de données climatiques modélisées et de reconstitutions historiques des conditions climatiques à l'aide des données sur les anneaux de croissance des arbres. Les données de stations météorologiques ont révélé que les flambées de dendroctones apparaissaient pendant des périodes de chaleur prolongées qui se traduisaient par une sécheresse. Les indices de sécheresse ainsi que les températures automnales et printanières des 150 dernières années au moins ont pu être reconstituées à l'aide des données relatives à l'épaisseur des anneaux de croissance des arbres. Bien qu'elle soit de plus en plus fréquente aux limites de l'habitat actuel des dendroctones (p. ex. le parc national Banff), la sécheresse est une condition qui persiste dans le centre de la Colombie-Britannique, où les flambées ont eu une durée beaucoup plus longue. Malgré le fait que les températures reconstituées à partir des anneaux de croissance des arbres semblent osciller davantage, celles prédites à l'aide des modèles indiquent une augmentation assez linéaire, les températures printanières étant les plus changeantes. La sécheresse a augmenté de façon similaire. Comme celle-ci diminue considérablement la résistance des arbres face aux attaques de dendroctones, et que les chaudes températures printanières sont essentielles à la survie des larves, on peut s'attendre à ce que le climat aux limites de la flambée de dendroctones actuelle continue de fournir les conditions idéales pour d'autres flambées de dendroctones.

Les liens entre l'apparition des flambées de dendroctones et l'historique des incendies ont été évalués à l'aide de diverses méthodes propres à la dendrochronologie. La datation des cicatrices de feux sur le plateau de la région de Cariboo-Chilcotin au centre de la Colombie-Britannique a révélé que les feux étaient moins fréquents au XXe qu'au XIXe siècle. Cela pourrait expliquer pourquoi les flambées des années 1930 et 1940, ainsi que des années 1970 et 1980 ont été plus considérables dans cette région. Les peuplements des régions caractérisées par des régimes de feux dont l'intensité était faible ou variable ont été plus souvent touchés par des flambées que les régions où les feux entraînent le remplacement des peuplements. Parmi les peuplements qui ont pris naissance à la suite de feux donnant lieu au remplacement des peuplements, on note que le temps écoulé depuis le feu a une grande incidence sur la fréquence des flambées de dendroctones : celles-ci étaient plus fréquentes dans les peuplements 50 à 100 ans après un feu, soit lorsque les

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arbres sont moins résistants aux attaques des dendroctones et que les tissus du phloème favorisent la croissance des dendroctones.

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1 Introduction

1.1 Mountain pine beetle

Mountain pine beetle, *Dendroctonous ponderosae* Hopkins (Coleoptera: Curculionidae), lives in pine forests from northern British Columbia to northern Mexico. In British Columbia, lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) is the most common host, but ponderosa pine (*P. ponderosa* Laws), whitebark pine (*P. albicaulis* Engelm.), western white pine (*P. monticola* Dougl.) and limber pine (*P. flexilis* James) are also suitable hosts (Furniss and Carolin 1977). Apart from the dispersal of adults, all life stages of the beetle occur within the host trees' inner bark. Beetles disperse and colonize living host trees in mid- to late summer by boring through the outer bark. Females carve out J-shaped vertical galleries under the bark and, once mated, deposit eggs in niches along the main gallery. Hatched larvae feed on the phloem, mining lateral galleries as they go. Larvae usually overwinter as late-instar larvae and complete development to adults the following spring (Reid 1962). However, at higher elevations and probably at the more northern reaches of the beetle's range where summers are cooler, two years may be required for the beetle to complete its lifecycle (Amman 1973).

In its endemic phase, mountain pine beetle, along with a complex of other bark beetles, normally colonize the oldest, most stressed trees scattered throughout a forest, which usually cannot make enough resin to resist beetle entry into the host (Safranyik and Carroll 2006). Colonization by these bark beetles hastens the death of an already compromised host over several years. However, mountain pine beetle populations occasionally increase enough to permit pheromone-mediated mass-attacks that overwhelm the natural defences of healthy trees and kill mature lodgepole pine over many thousands of hectares (Safranyik et al. 1975; Raffa and Berryman 1983). Trees infested by mountain pine beetle usually die within one or two years because lateral galleries mined by the larvae and associated symbiotic fungi carried into the tree by mountain pine beetle disrupt the flow of water and nutrients. The loss of moisture transport in attacked trees causes foliage to fade from light green to yellow and red in the year following attack, when most beetles have completed their lifecycle and dispersed from the tree. During aerial assessments of forest insect and disease conditions, surveyors map areas where host foliage has changed colour and use this information to quantify the extent of beetle outbreaks.

Outbreaks of mountain pine beetle are natural disturbances that play a critical role in development, senescence, and rebirth of western North American pine stands. They are part of a cycle that helps to maintain biologically diverse and functionally healthy forest landscapes (Axelson et al. 2009). However, the patterns of mountain pine beetle outbreaks, and, indeed, of many natural forest disturbance processes, appear to be changing. Scattered historical accounts indicate mountain pine beetle outbreaks occurred in parts of British Columbia in the early 1900s. Annual aerial surveys of forest insect and disease conditions began in 1959; these detected a beetle outbreak from the mid-1970s to the mid-1980s that killed about 2 million ha of mature pine forests in western Canada. Aerial surveys indicate that the current beetle outbreak, which started in 1999, has spread far further than that, killing over 10 million ha of mature pine forests in western Canada. The socioeconomic impacts of such large outbreaks are enormous, particularly in British Columbia where wood from lodgepole pine forests comprises 25% of the province's timber supply. In addition to extensive timber losses, widespread tree mortality caused by beetle outbreaks will increase the risk of future wildfires and alter successional trajectories, watershed hydrology, and nutrient cycles (McCullough et al. 1998).

More widespread mountain pine beetle outbreaks in western Canada may be due to forest management (e.g., harvest regulation, fire suppression) having increased the abundance of susceptible lodgepole pine forests and because warming climates are expanding the geographic

range within which the beetle can complete its lifecycle (Logan and Powell 2001; Carroll et al. 2006). Understanding how these factors drive change in the dynamics of beetle outbreaks requires knowing more about the history of beetle outbreaks than the limited scope of historical record. Deducing the history of beetle outbreaks over a much longer time will help to determine if the extent of recent beetle disturbances is well outside its natural range of variability, and if this can be related to recent forest and climate change. Little information exists about the frequency and extent of mountain pine beetle outbreaks during past centuries in British Columbia and Alberta.

1.2 Tree-ring evidence of mountain pine beetle outbreaks

Aerial surveys and historical accounts of beetle outbreaks can help to reconstruct recent outbreak history, but archives before 1959 are scant, inconsistent, and unreliable. Natural archives that chronologically store biological processes (e.g., tree-ring growth, ice cores, geological processes of soil and rock layering) can be used to date past disturbances over much longer time scales. This study uses dendrochronology (the study of tree-ring growth patterns) to reconstruct the historical occurrence of beetle disturbances in pine forests. Analysis of tree-ring growth patterns has been used extensively to study historical outbreak patterns of many defoliating forest insects (Swetnam and Lynch 1993; Speer et al. 2001; Bergeron et al. 2002; Burleigh et al. 2002; Zhang and Alfaro 2002; Campbell et al. 2007), but much less has been used for studying bark beetle outbreak patterns (Veblen et al. 1991a). Although Heath and Alfaro (1990) attributed radial growth releases to thinning caused by beetle outbreaks in a single stand in central British Columbia, no studies have used a dendrochronological approach to determine mountain pine beetle outbreak patterns over larger spatial and temporal scales.

During a beetle outbreak, some lodgepole pine can resist or survive attacks. Surviving trees undergo a growth increase or "release" period (Figure 1) commensurate with the initial density of the stand, the basal area of trees killed by beetles, and site conditions. Typically, bark beetle signals in tree-rings of surviving trees consist of release periods in response to the thinning of the stand by beetles. We propose that growth release periods may begin abruptly, indicating epidemic populations acting on a highly susceptible host, or gradually, indicative of low mountain pine beetle populations acting on more resistant stands. These release periods can be used to identify mountain pine beetle outbreaks in stands.
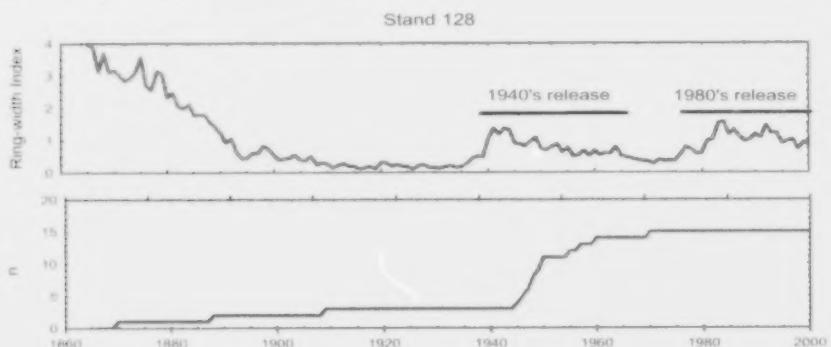
Figure 1. Mean standardized chronology of tree-ring widths indicating two stand-wide disturbances attributable to mountain pine beetle outbreaks in stand 128 in the Cariboo-Chilcotin Plateau, central British Columbia. Sample depth (i.e., number of tree-rings in any given year) is given by the bottom graph.

1.3   Project objectives

This research project used well-established methods of dendrochronology to reconstruct the frequency, intensity and extent of mountain pine beetle outbreaks during past centuries, and to determine if variations in climate or fire regime may have contributed to a change in beetle outbreak dynamics.

This project had three main objectives:

To reconstruct the spatial and temporal history of mountain pine beetle outbreaks over the last two centuries in British Columbia, using dendrochronological methods

Specifically:

Identify the occurrence of beetle outbreaks based on accelerated growth periods (i.e., growth releases) in tree rings from surviving trees;

Determine the return rate of beetle outbreaks over the last two centuries;

Quantify the intensity of outbreaks (measured by the slope of the ascending portion of the growth release period);

Quantify the magnitude of the growth releases;

Compare patterns of outbreak identified through growth release data with corroborating evidence of outbreaks (documentary records, death dates of beetle-killed trees, and beetle scar dates.

To describe relationships between mountain pine beetle outbreaks and climate

Specifically:

Summarize instrumental weather station data associated with periods of documented mountain pine beetle outbreaks;

Reconstruct historical climate conditions from tree-ring data;

To describe relationships between mountain pine beetle outbreaks and fire history

Specifically:

Summarize relationships between beetle outbreaks and fire severity and frequency;

Determine the probability of beetle outbreaks as a function of time since last stand-replacing fire.

2 Methods

2.1 Tree-ring reconstruction of historical mountain pine beetle disturbances in British Columbia and Alberta

2.1.1 Study design and field sampling

Increment cores and disks were obtained from lodgepole pine and non-host species such as Douglas-fir and Engelmann spruce in 121 lodgepole pine-dominated stands throughout British Columbia and Alberta (Figure 2). Some tree-ring and associated stand data were obtained from previous and ongoing studies, while others were collected in the field between 2003 and 2005.

One increment core, or disc, was collected from 10 hosts and up to 10 non-host trees. The largest (and presumably oldest) trees in a stand were selected for sampling as they provide the longest tree-ring record. Oldest trees were identified based on size, high degree of bark rugosity, presence of beetle scars, and old gnarled branches near the crown of the tree. Increment cores and disks were taken at breast height (1.3).

2.1.2 Preparation, measurement, and cross-dating of new samples

All increment cores and discs collected from lodgepole pine and non-hosts in 2004 were air-dried and prepared in the laboratory following standard dendrochronological procedures (Stokes and Smiley 1968; Swetnam 1987). Cores were mounted on wood planks and sanded with progressively finer sand paper (grits 220 to 600) to enhance the boundaries between annual growth rings.

Mounted increment cores and tree discs were scanned. The scanned images of increment cores and basal disks were uploaded into WinDendro[TM] (v.2002a, Regent Instruments Inc., 2003). This tree-ring image processing software automatically marks annual growth rings based on differences in light intensity, which works well for conifers as they show high contrast between rings. However, some manual adjustment was required (e.g., addition of markers to faint growth rings and deletion of false rings). The distance between annual growth rings was measured to the nearest 0.01 mm.
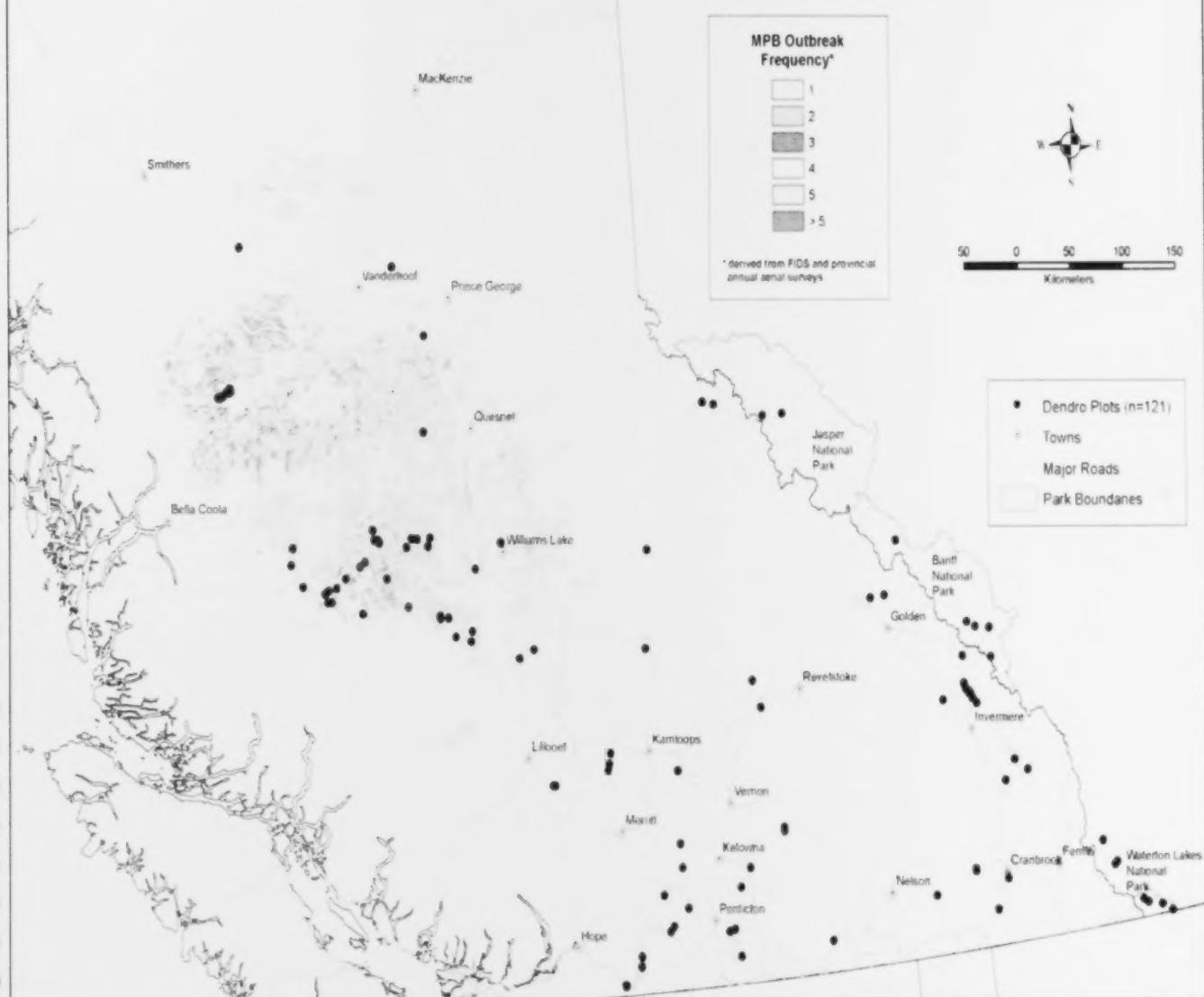
Figure 2. Location of stands from which tree-ring data was collected in British Columbia and Alberta. Coloured areas indicate the number of years an outbreak was recorded during aerial survey.

The set of ring width measurements for each core (a tree-ring series) was compared to the mean ring width series of all cores for a stand using the program COFECHA (developed by the Laboratory of Tree Ring Research, University of Arizona-Tucson; Holmes 1983). This program helps to detect measurement and dating errors by computing correlation coefficients between overlapping 50-year segments from individual tree-ring series and a reference master chronology. Tree-ring series that did not cross-date well with other samples in a stand (i.e., $r < 0.500$) were checked for dating or measurement errors and corrected as needed. Series that remained poorly correlated with other samples in a stand were eliminated from the dataset. Detailed notes on the dating corrections were stored with the final file of dated tree-ring series.

The computer program ARSTAN (Cook 1985, Cook & Holmes 1986) was used to produce a mean standardized tree-ring width chronology (i.e., growth averaged over several trees in a stand) for each species in each stand sampled. Dated tree-ring series in each stand were standardized by fitting a horizontal line through the mean of each tree-ring series (i.e., ring width was divided by the mean series ring width). Other functions have commonly been used to standardize tree-ring series but standardizing by a horizontal straight line preserves the long-term growth trend necessary to identify dramatic and sustained increases in growth generated by canopy disturbances (Veblen et al. 1991a; Eisenhart and Veblen 2000). Using an arithmetic mean, standardized tree-ring series were averaged together to produce a mean chronology for each stand. Variance in tree-ring width was stabilized using a negative exponential curve. Chronologies of tree-ring widths for individual trees and the mean standardized chronology (created by ARSTAN) were graphed.

2.1.3 Tree-ring reconstruction of beetle outbreak history

Releases in growth that could be attributed to stand thinning during beetle outbreaks can be visually determined. However, we used the program JOLTS (Holmes 1999) to identify growth releases on individual trees (hosts and non-hosts) in a stand, as it objectively scores releases. We defined a growth release as 25 percent increase in growth (i.e., growth release factor = 1.25) in mean ring width over a 10-year period. This means that for each year, we calculated a mean of the next (forward) 10 rings and the mean of the past (backward) 10 rings. If the ratio of the forward mean ring width to the backward mean ring width exceeded 1.25, we considered that year to be a release year. The JOLTS program was also run to detect a 50% and a 100% (i.e., doubling) increase in radial growth. For illustration purposes, a portion of the data generated from these JOLTS runs was summarized graphically and in tables.

2.1.4 Corroborating evidence of beetle outbreaks

2.1.4.1 Documentary archives (i.e., field data, local knowledge, and aerial survey data)

We overlayed the locations of the sample stands onto digitized maps of beetle infestation areas using ArcInfo GIS. Evidence of beetle infestations in the GIS database came predominantly from annual aerial surveys, although some field data and local knowledge of beetle outbreaks were mapped prior to 1962. To account for error in mapping of infestation polygons and in geographic locations of sample sites (some older sites were mapped before the availability of GIS), we allowed for a 500-m buffer area around each stand location. If a stand (including the 500-m buffer) intersected with mapped polygons of beetle infestation for a given year, we considered that stand to have been infested. Data were summarized in a table and compared to periods of tree growth releases.

2.1.4.2 Pine death dates

Temporal distributions of beetle-killed trees are another way to determine the occurrence and timing of a mountain pine beetle outbreak. Cookies and increment cores were collected from dead trees in the Cariboo-Chilcotin Plateau of central British Columbia. Standard dendrochronological crossdating procedures (see outline of procedure above; COFECHA, Holmes 1983) were used to compare tree-ring width series of dead trees to tree-ring width series of living trees. Correlation analysis of 50-year ring width segments were used to match tree-ring series to determine the tree death dates. Frequency distributions of host death dates were graphed and compared to tree-ring release data.

2.1.4.3 Dated beetle scars

Host trees that resist mountain pine beetle attacks generate resins and produce a wound response that leave anomalies in the wood. Both trace resin and wound responses can be seen in cross

sections cut from the stems of host trees. These anomalies in the wood can be dated by recording which annual growth ring they occur in. The dates of beetle scars were tallied among cross-sections taken from lodgepole pine in central British Columbia. We graphed the death dates for the entire region and compared death dates to tree-ring releases by overlaying them onto the master tree-ring chronology produced for each stand. Although some scars in the cross sections may be caused by infestation by other beetles, there is a high probability that they are caused by mountain pine beetle during outbreak years.

2.2 Historical climate associated with beetle outbreaks, and future climate conditions

2.2.1 Weather associated with past beetle outbreaks in British Columbia and Alberta

Daily instrumental temperature and precipitation data were extracted from the Environment Canada meteorological database for two study areas: one in the Cariboo-Chilcotin Plateau of central British Columbia and another in Banff National Park. Daily instrumental temperature (°C) data were averaged and precipitation (mm) data were summed to obtain monthly values for each year which weather station data was available. Seasonal and annual temperature and precipitation values were calculated from monthly values. Following Ung et al. (2001), a monthly aridity index (i.e., drought index) was calculated using Thornwaite's monthly potential evapotranspiration (Dunne and Leopold 1978) minus monthly precipitation. For the Cariboo-Chilcotin Plateau study area, we averaged temperature and precipitation data over three weather stations that were located in the Interior Douglas-fir (IDF dk) biogeoclimatic zone: Big Creek (51° 43'N, 123° 01'W; elevation: 1 128 m asl.), Tatlayoko Lake (51° 39'N, 123° 01'W; elevation: 853m asl.), and Williams Lake (52° 11'N, 122° 03'W, elevation: 940 m asl.). Using these stations, a chronology of weather variables was constructed from 1904 to 1982. Instrumental weather data were summarized for a single weather station in Banff National Park (51°11'N, 115°34'W; elevation: 1 384 m asl., and 51°12'N, 115°33'W; elevation: 1397 m asl.) to construct a chronology of temperature and precipitation data for the period 1896 to 2003.

Interactions between oceans and atmosphere can affect air mass circulation and climate over vast geographical areas. The Pacific Decadal Oscillation (PDO) is a 40- to 50-year cycle in north Pacific sea surface temperatures that can cause similar oscillations in continental climates. Unlike other sources of climate variability, the PDO tends to shift abruptly from warmer to cooler states (Gedalof and Smith 2001). The last major positive shift occurred from 1976 to 1977, and is thought to have generated warmer regional climates. We compared published, standardized PDO records (actual measurements and tree-ring reconstructed values; D'Arrigo et al. 2001; Biondi et al. 2005) to standardized monthly, seasonal and annual variations in temperature and precipitation in the Cariboo-Chilcotin Plateau of central British Columbia and Banff National Park, Alberta. We also compared chronologies of radial tree growth with the PDO.

2.2.2 Beetle outbreak occurrence by biogeoclimatic zone

The frequency of beetle outbreaks among stands sampled was summarized by biogeoclimatic zone. To determine which biogeoclimatic zone each stand occurred in, we used ArcInfo GIS to overlay point data of sampled stands with a map of biogeoclimatic subzones in British Columbia. Alberta stands were grouped separate from British Columbia stands.

For each stand sampled, we considered a beetle outbreak to have occurred if at least 30% of the trees in a stand sustained a growth increase. Using results of JOLTS, these were trees that grew by at least a 25%. For each biogeoclimatic zone, the occurrence of outbreaks was tabulated and the percentage of stands having an outbreak was reported.

2.2.3 Radial tree growth and climate

Quantifying relationships between radial tree growth and weather over several decades provides a means of assessing the effects of local climate on tree diameter growth. This information can be used to reconstruct historical climates prior to instrumental weather records. In this project, such information was necessary to account for the confounding effect of climate on tree growth, so that growth releases due to mountain pine beetle can be confidently identified.

Analyses of relationships between tree growth and climate were conducted on a subset of all the tree-ring data collected over British Columbia and Alberta. We used lodgepole pine and Douglas-fir tree-ring series for two study areas: the Cariboo-Chilcotin Plateau in central British Columbia and Banff National Park, Alberta (the same lodgepole pine used in descriptions of weather in section 2.2.1). Lodgepole pine tree-ring series were collected from beetle-affected lodgepole pine-dominated stands, and those of Douglas-fir were collected from rocky slopes. In the Cariboo-Chilcotin Plateau, we combined tree-ring series from 12 low-elevation lodgepole pine stands and combined tree-ring series of Douglas-fir from four sites. In Banff National Park, lodgepole pine tree-ring series were combined from two stands and Douglas-fir were collected from a single site.

The program ARSTAN was used to calculate mean standardized chronologies of tree-ring width for lodgepole pine and Douglas-fir in each of the two study areas. Both lodgepole pine and Douglas-fir trees often grow rapidly when they are young. Because we want to use the tree-ring width series from these species to examine trends in climate, it is necessary to remove the effect of tree size/age on tree growth. The program ARSTAN was used to remove the size/age trend (using a negative exponential curve, a regression line with a negative slope, or a horizontal line) from each tree-ring series. The resulting deviations from this curve were standardized to produce a series of tree-ring width indices, which were averaged to produce a mean standardized chronology for each species at each study area. Biological persistence (i.e., autocorrelation) was removed from standardized tree-ring measurements (using a first-order autoregressive model) to eliminate variation not due to climate (Fritts 1976). The resulting residual chronologies were used to test for relationships among tree-ring width and climate.

Relationships between radial tree growth (i.e., residual ring widths of lodgepole pine and Douglas-fir) and monthly climate (i.e., precipitation and temperature over at least 75 years) were analyzed by means of correlation analysis and response function analysis using the program PRECON (Fritts 1976). The instrumental monthly temperature and precipitation data entered into the analyses spanned from 1904-1982 for the Cariboo-Chilcotin Plateau region and from 1903-2002 for Banff National Park. PRECON was also run to test for relationships between drought in growing season months (i.e., May to October), and tree-ring width of lodgepole pine and Douglas-fir (see above section 2.2.1 for the method used to calculate aridity indices). To account for numerical and biological persistence in the tree responses to climate, we employed an 18-month dendroclimatic window, going backwards from October of the current growth year to the previous May.

2.2.4 Dendrochronological reconstruction of historical climate from tree rings

Variations in tree-ring widths were used to reconstruct historical climate condition in the Cariboo-Chilcotin Plateau and Banff National Park. We used the results of response function analyses in the previous runs of PRECON (see section 2.2.2) to determine which monthly values of precipitation, temperature, and aridity could be reconstructed from tree rings. The results of response function analyses rather than correlation analyses were used because the multiple regressions on the principal components of orthogonized climate data and the bootstrapping techniques used in response function analysis make it a more robust approach for testing the

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significance of relationships between tree-ring width and climate (Guiot 1991; Fekedulegn et al. 2002). Among the monthly variables that were significantly related to tree-ring width, we chose to reconstruct the history of those that might also affect the impact that beetle outbreaks have on lodgepole pine. Periods of drought stress are thought to reduce the resistance of pine trees to attack by beetle outbreaks. Cold temperatures from October to June can induce significant levels of mountain pine beetle mortality (Safranyik and Carroll 2006). Simple regression analyses on monthly climate data were used to develop the models necessary to reconstruct a history of drought (June) and cold season temperatures (October to May) from tree rings in the Cariboo-Chilcotin Plateau and Banff National Park. Standard regression diagnostics were used to test the assumptions of least-squares regression, and outliers were removed to improve model fit. Verification of our models was undertaken in manner similar to the "leave-one-out" method of Blasing et al. (1981), where each odd year of the measured climate variable is estimated using the remaining even years of data. Instrumental climate data included in the analyses spanned from 1904 to 1982 for the Cariboo-Chilcotin, and 1896 to 2003 for Banff National Park. Wavelet spectral analysis (Torrence and Campo 1998) of climate conditions reconstructed from tree rings was used to determine if the frequency of drought has changed over the last two centuries.

2.2.5 Projections of future climate in the stands sampled over British Columbia and Alberta

In all the stands from which we collected increment cores for dendrochronological analyses, we used ClimateBC v.2.0 (Wang et al. 2006) to estimate historical climate and predict future climate conditions. Historical data were estimated based on interpolated normals (1961-1990) from existing weather stations and future climate conditions were predicted based on a climate change scenario described by the CGCM2-A2x global circulation model (Flato et al. 2000). By entering the latitude, longitude, and elevation of each of our sample stands into ClimateBC, we generated a set of monthly, seasonal, and annual climate variables that were unique to each stand for the reference period 1961-1990. Based on this reference period and the CGCM2-A2x scenario, we predicted future climate for the 2020s, 2050s, and 2080s. The following variables were estimated for each stand: mean annual temperature (MAT, °C) and extreme minimum temperature over 30 years (Extr. Cold, °C); mean winter, summer, and fall temperatures; mean annual precipitation (MAP, mm) and mean summer precipitation (MSP, mm); and summer aridity index. Because temperatures from October to the following May have the greatest affect on beetle overwintering mortality, this data was averaged over all stands and graphically presented to provide a general overview of climate change within the current range of mountain pine beetle outbreaks. The data were then averaged over biogeoclimatic zones to examine how historical conditions varied by region and to detect differential responses to climate change. Data were summarized for 12 groups of biogeoclimatic zones in British Columbia: (ESSF dc, dm; ESSF mw; ICH dm ; ICH mk,mw; ICH vk, wk; IDF dk; IDF dm; MS dk; MS dm; MS xk, xv; SBPS xc; SBS dk, dw, mc). Climate data from Alberta were grouped and summarized separately. We also examined changes in climate more closely in the Cariboo-Chilcotin Plateau, where outbreaks have occurred for at least 150 years, and in stands at the current edge of the outbreak range: Banff National Park and Prince George.

2.3 Mountain pine beetle outbreak and fire history

2.3.1 The history of low intensity surface fires in central British Columbia

Disturbances other than mountain pine beetle could cause an increase in the radial growth of trees and affect our ability to detect growth releases attributable to mountain pine beetle. It has been suggested that low-intensity surface fires could generate a growth release that could be mistaken for a beetle outbreak. To test this, we reconstructed the history of low-intensity surface fires from fire scar data collected in the Cariboo-Chilcotin Plateau in central British Columbia. Cross-

sections of trees with visible fire scars were collected from the area. Using standard cross-dating methods (see above), fire scars on each cross-section were dated to a particular year. A frequency distribution of fire scars was constructed to examine when fires were most frequent in this region. For each stand, the year of the fire scar was overlaid onto graphs of master chronologies so that we could check for growth releases associated with the occurrence of a fire around this time.

2.3.2 Relationships between beetle outbreak occurrence and fire severity and frequency

To describe the relationships between the occurrence of beetle outbreaks and fire severity or intensity, we overlaid an ArcInfo data point layer of our sample plots onto a digitized map layer of fire regimes for southern British Columbia (Blackwell, B.A. and Associates Ltd et al. 2003). For stands further north, expert knowledge about the characteristics of fire regimes in biogeoclimatic zones (Brad Hawkes, unpublished data) was relied upon to determine fire frequency and fire severity. Stands were grouped by fire frequency and fire severity.

Results from JOLTS runs (growth release factor 1.25) on individual trees within a stand were used to determine the percentage of trees that had growth releases within two beetle outbreak periods: the 1930s-1940s (i.e., releases between 1930-1960) and the 1970s-1980s (i.e., releases between 1970-1999). An outbreak was considered to occur in a stand if more than 30% of trees had at least a 25% increase in radial growth during the outbreak period. The frequency of outbreaks by fire severity class and fire frequency class were tabulated.

2.3.3 Probability of beetle outbreaks as a function of time since last stand-replacing fire

We used dendrochronological methods to determine relationships between the occurrence of beetle outbreaks and the time since the last stand-replacing fire. First, we determined which lodgepole pine stands originated from a stand-replacing fire. Fires cause the release of massive amounts of lodgepole pine seed from their serotinous cones. Because of this, dating the pulses of tree establishment provide a good way to approximate stand age, and thus approximate the time since the last stand-replacing fire (Johnson and Gutsell 1994). We determined the germination dates of each tree in stands from which we collected increment cores by dating each ring and counting backwards, from the sample towards the pith. Because all samples were collected at breast height, this represents an estimate of germination date. Stand-replacing fire events were considered to have occurred when at least 40% of the trees sprouted within a 40-year period. The decade in which peak germination occurred was used to calculate the time since the last stand-replacing fire disturbance.

Results from JOLTS runs (growth release factor 1.25) on individual trees within a stand were used to determine the percentage of trees that had growth releases within two beetle outbreak periods: the 1930s-1940s outbreak (i.e., releases between 1930-1960) and the 1970s-1980s outbreak (i.e., release between 1970 and 1999). An outbreak was considered to occur in a stand if greater than 30% of the trees had at least a 25% increase in radial growth during the outbreak period. We grouped stands by the following time-since-fire classes: 10-59 years, 60-99 yrs, 100-149 and ≥150 years. We pooled growth release data from each outbreak period (i.e., 1930s-1940s and 1970s-1980s) to determine relationships between outbreak frequency and time since fire.

3 Results

3.1 Reconstructing beetle outbreaks from tree rings

To reconstruct beetle outbreaks, we used tree-ring data from 85 of the 121 stands from which increment core samples were obtained. Samples from the remaining 36 stands could not be cross-dated, or the number of samples per stand was too small to reliably determine the stand-level disturbances caused by beetle.

Mean standardized chronologies of radial growth were produced for all 85 stands to visualize the overall effect of stand-wide canopy disturbances in lodgepole pine-dominated stands. Mean chronologies were produced for both lodgepole pine and non-hosts if they occurred in a stand. The length of mean chronologies of lodgepole pine radial growth ranged in length from about 80 to 370 years (average = 132 years), with lodgepole pine at Saskatchewan Crossing in Banff National Park being the oldest trees sampled. Non-host chronologies were constructed from Douglas-fir, Engelmann spruce, white spruce, western hemlock, western larch, and subalpine fir. Non-host chronologies ranged from 55 to 375 years (average = 127 years). The longest non-host chronology was created from Douglas-fir trees in Savona Provincial Park.

3.1.1 Details of beetle outbreak reconstructions in selected stands

Identification of growth releases on individual trees was automated using the program JOLTS. The frequency of trees showing a release in any particular year was graphed and outbreaks were considered to occur when at least 30% of the trees in a stand were releasing at the same time. We examined patterns of growth releases in detail for four stands (Stands no. 128 and 130 in the Cariboo-Chilcotin Plateau, one in Banff National Park, and one in Prince George). The stands were selected to represent an area where outbreaks are known to have occurred for a long time (the Cariboo-Chilcotin Plateau of central British Columbia) and for two areas at the current edge of mountain pine beetle outbreak range (Banff National Park, Alberta, and Prince George, British Columbia) (Figure 3).

Stands of the Cariboo-Chilcotin Plateau are dominated by lodgepole pine and most contained lodgepole pine of varying ages/cohorts. Aerial survey data indicated a mountain pine beetle outbreak in this region between 1977 and 1983. Local knowledge also indicated a widespread beetle outbreak in this region during the late 1930s and 1940s. Dated fire scars on trees indicated surface fires between 1871 and 1896. Stand 128 (Figure 3a) appears to have had three major pulses of tree recruitment: 1900-1910, 1925-1930, and 1935-1955. The 1977-1983 outbreak was the cause of death for the oldest trees in the stand (Figure 3a); the surviving trees were younger. Using JOLTS, we determined the frequency of trees with 25%, 50%, and 100% increase in growth. We detected four pulses of increased growth in stand 128: around 1905 and between about 1935-1940, 1955-1960 and 1971-1990. The growth increases of the 1970s and 1980s are the most pronounced and are associated with a mountain pine beetle outbreak. At least 30% of trees had growth releases during this time, even when a release was defined as a doubling of growth. Releases prior to the 1970s were rarer, possibly because stand disturbances were less severe then. Releases among established trees and recruitment of several lodgepole pine from 1935-1940 suggest a stand-wide disturbance event, probably a mountain pine beetle outbreak.

Stand 130 (Figure 3b) of the Cariboo-Chilcotin Plateau contained many more older trees than stand 128. Aerial survey data indicated a beetle outbreak in this stand between 1978 and 1983. A low-intensity surface fire occurred in 1917 (determined from dated fire scar data), but no growth release was associated with this fire. Again, tree-ring data indicated three periods of growth releases that occurred approximately in the 1940s, the 1960s, and in the late 1970s and early 1980s. The 1940s and 1970s-1980s growth releases were most pronounced. Aerial survey data,

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field data, and death dates of beetle-killed trees provide corroborating evidence of a 1970s/1980s mountain pine beetle outbreak. Thus, growth releases during this time were caused by a mountain pine beetle outbreak in these stands.

A stand sampled in Banff National Park had trees ranging in age from about 118 to 168 years. Two distinct periods of recruitment occurred in this stand (Figure 3c). The first probably resulted from a stand-replacing fire between 1830 and 1840. Documentary records for the park indicate two periods of beetle outbreak: 1940s-1960s and 1970s-1980s. Two major pulses of lodgepole pine growth occurred in the 1960s and late 1970s/early 1980s and correspond well to a stand-wide disturbance by a mountain pine beetle outbreak at that time.

The stand sampled near Prince George is considered to be near the current (2006) northern limit of mountain pine beetle outbreaks. Aerial surveys did not document the occurrence of beetle outbreaks in this stand until 2003. Lodgepole pines sampled in this stand were about 123 to 143 years old (Figure 3d). The close range in ages suggests they were recruited after a stand-replacing fire in the 1860s. Growth releases among lodgepole pine in this stand were not as pronounced as they were in either stands of the Cariboo-Chilcotin Plateau or Banff National Park. It was only during the late 1970s that at least 30% of trees had a release in growth (a 25% or 50% growth increase). Although a beetle outbreak during this time cannot be corroborated by aerial survey data, it is possible that a low-severity outbreak was not detected during aerial surveys.
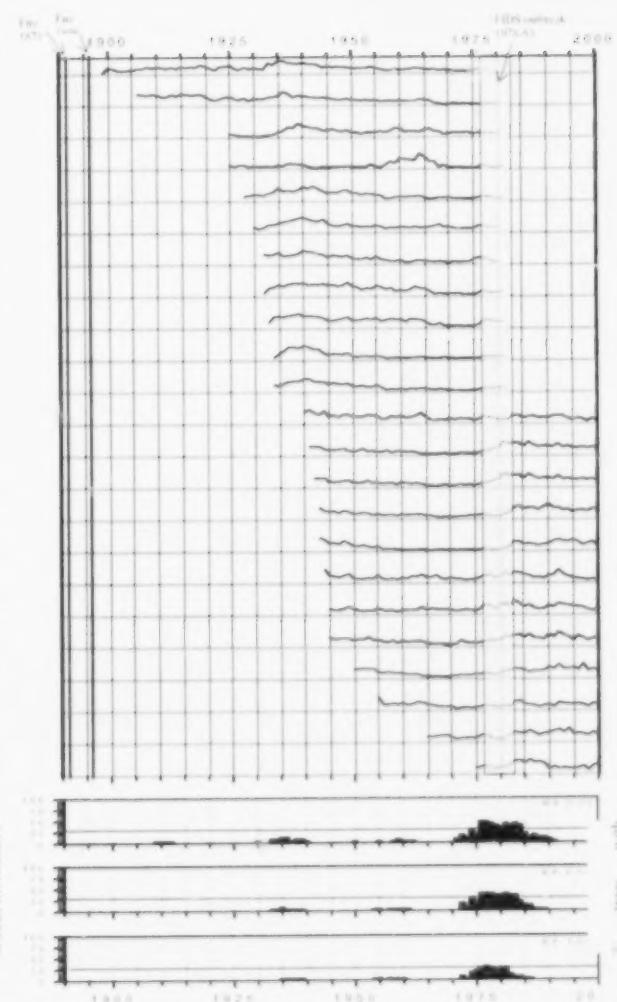
a) Cariboo-Chilcotin 128
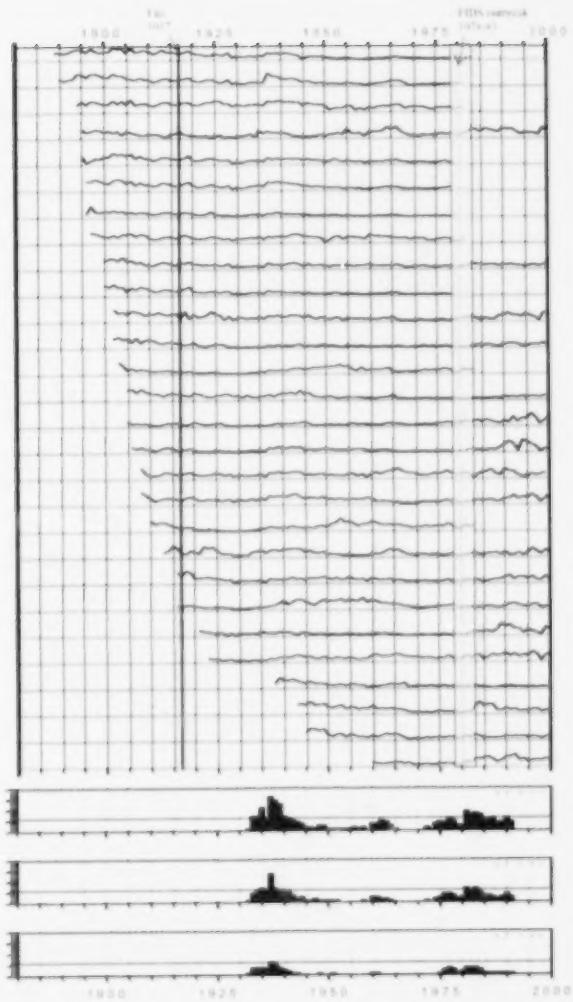
b) Cariboo-Chilcotin 130

Figure 3. Measured ring width indices for individual trees and frequency distributions of lodgepole pine growth releases for selected stands in British Columbia and Alberta. Frequency distributions are presented for 3 JOLTS runs using a growth release factors (R.F.) of 0.25, 0.50, and 1.0, which indicate at least a 25%, 50%, and 100% increase in growth, respectively.
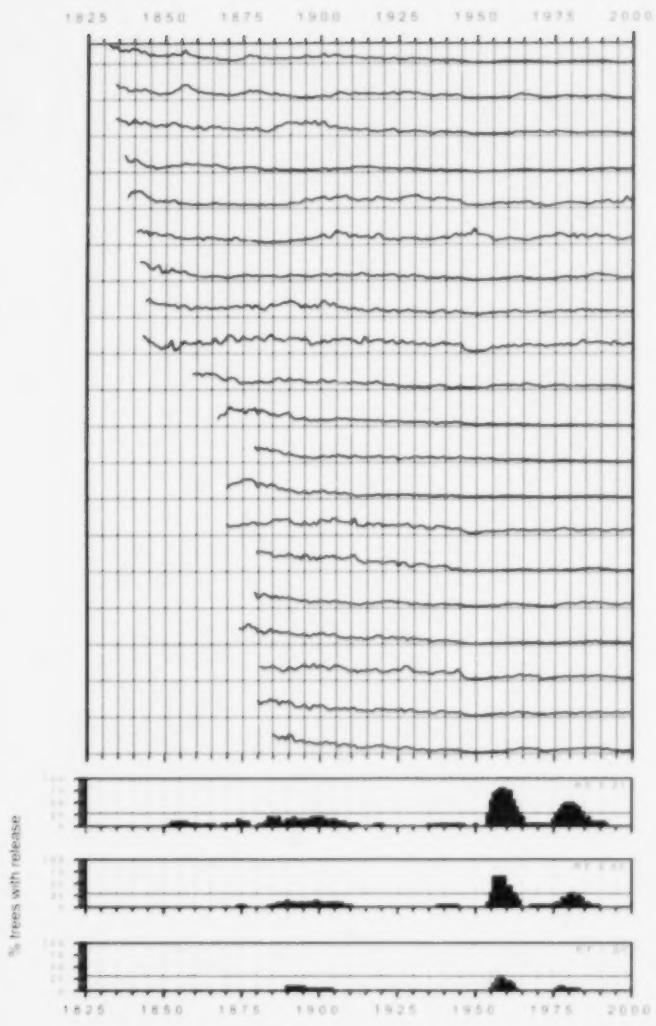
c) Banff National Park
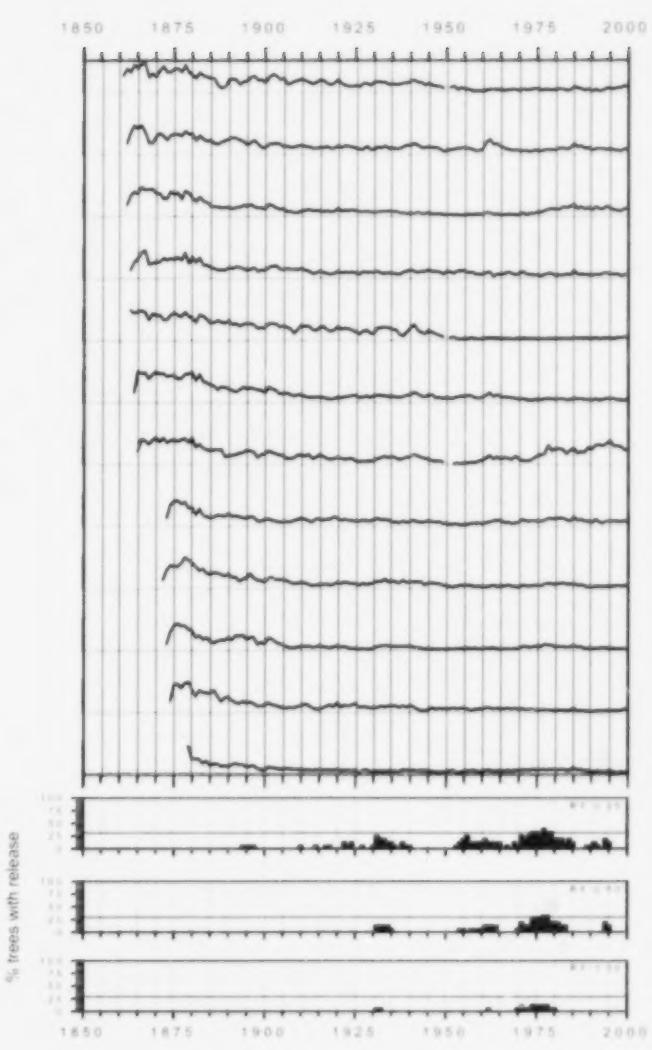
d) Prince George

Figure 3. (cont.)

3.1.2 Beetle outbreak reconstructions in British Columbia and Alberta

Growth release patterns of lodgepole pine and non-host trees were used to reconstruct the occurrence of beetle outbreaks over all 85 stands sampled in British Columbia and Alberta. Using these graphs, an outbreak period was defined as being at least 3 consecutive years of growth releases with more than 30% of the trees in a stand released at the same time, with an allowance for 1 or 2 years in which less than 30% of trees showed a release. The outbreak periods were summarized as floating bar graphs (Figures 4 [host] and 5 [non-host]) and characteristics of growth releases attributable to beetle outbreaks were tabulated (Tables A1 and A2).

Major growth releases caused by stand-wide disturbances were detected from the mid-1800s to the present. A few stands contained trees old enough for us to detect growth releases prior to 1850 (Figures 4 and 5). Growth releases synchronous over a significant proportion of the stands and over a large area suggest a widespread disturbance that is consistent with a mountain pine beetle outbreak. The 1970s-1980s outbreak is well-documented and well-represented by growth release data. Widespread synchronous growth releases in the 1930s and 1940s likely also result from a poorly documented widespread outbreak (although local knowledge for some areas indicate an outbreak then). Growth release data suggest that the 1940s outbreak was just as widespread as the 1970s-1980s outbreak (Figures 4, 5, and 6). About 10% of stands had significant growth releases in the 1960s (Figure 6). Although an outbreak is not well-documented in the aerial survey data during this time, local knowledge indicates that localized beetle outbreaks occurred during the 1960s. We found that 25%-30% of the stands we sampled also had periods of increased growth in the 1870s and 1900s (Figure 6). In most cases these releases occurred well after tree establishment and do not represent early rapid tree growth (especially among lodgepole pine). Thus, like releases during the 1960s, releases during the 1870s and 1900s may also be due to localized beetle outbreaks. In the Cariboo-Chilcotin Plateau, frequent fires have maintained the dominance of lodgepole pine on many sites for at least two centuries. Among some of the oldest stands in this region, we also observed substantial pulses of increased lodgepole pine growth caused by a stand-wide disturbance. Mountain pine beetle outbreaks may have occurred for at least the last two centuries in this region. In the northernmost stands sampled, we either detected very short growth release periods or none at all (Figures 4 and 6), suggesting that up until very recently, high beetle populations have been unable to persist in these regions.

Characteristics of growth releases attributable to mountain pine beetle outbreaks are summarized in Tables A1 and A2. Growth release periods associated with beetle outbreaks lasted up to about 20 years, although releases in Canal Flats lasted 33 years. Based on the interval between growth releases, we estimated the return-interval for mountain pine outbreaks to be between 30 and 40 years (Tables A1 and A2). JOLTS runs to detect trees with at least a 25% increase in radial growth indicated that average growth increases during a release period were generally much greater than 25% (Tables A1 and A2).

The slope of the increasing portion of a growth release period can provide an indicator of outbreak intensity. Beetles may colonize some stands quickly and kill hosts over a short time, resulting in a rapid and large release among survivors. In other stands, beetles may kill trees over a longer time, resulting in growth releases that last longer.

We calculated the slope of the increasing proportion of each identified release period by running JOLTS on the mean standardized chronology of lodgepole pine tree-ring width. We investigated the possibility that there was a relationship between outbreak intensity and stand location. Slope data for all stands were grouped by biogeoclimatic zone to check for differences in outbreak intensity that could be related to climate. Slope data were also examined more closely for the four

stands that we examined in greater detail in the previous section: stands 128 and 130 of the Cariboo-Chilcotin Plateau, Banff National Park, and Prince George. We found that the slope of the increasing portion of a growth release was highly variable and differences could not be explained by biogeoclimatic zone (Figure 8). When we looked at individual stands, we found that the slope of growth release was much steeper in stand 128 of the Cariboo-Chilcotin Plateau than in colder biogeoclimatic zones further north (stand 130 of the Cariboo-Chilcotin Plateau and Prince George). Slope values were similarly low in Alberta, suggesting their beetle outbreaks were less intense.

3.1.3 Frequency of beetle outbreaks by biogeoclimatic zone

We calculated the frequency of beetle outbreaks by biogeoclimatic zone based on growth release periods identified in the above section (Table A3). The 1940s outbreaks occurred most frequently (i.e., in 50%-56% of those sampled) in the IDF (dk and dm subzones) and ESSF (dc, dm, and mw subzones) biogeoclimatic zones. In Alberta and the SBPS zone of British Columbia, outbreak frequency was about 10% less. In moister and colder biogeoclimatic zones (i.e., ICH, MS, and SBS), outbreak frequency was 10% to 18% during the 1940s. In contrast, outbreaks in the 1970s-1980s were most frequent in Alberta and in the IDF, MS and SBPS biogeoclimatic zones of British Columbia (27% to 32%). Outbreaks were at least 20% less frequent in colder biogeoclimatic zones (i.e., the ESSF and SBS). As in the 1940s, outbreaks in the ICH zone were at least 10% less frequent than they were in other biogeoclimatic zones.

3.2 Corroborating evidence of beetle outbreaks

3.2.1 Documentary archives

Before 1962, evidence of past mountain pine beetle infestations came from digitized field observations of infestations and local knowledge. In the area sampled, this documentary evidence indicated infestations from the late 1920s to 1940. Earlier information is not available. In this period, outbreaks were found in Kootenay National Park, Tunkwa and Savona Provincial Parks near Kamloops, and in the Okanagan near Penticton (Figure 7). In all of these stands, we detected substantial increases in the radial growth of surviving trees that could be attributed to canopy disturbances caused by concurrent beetle outbreaks (Figures 4 and 5).

Since 1962, aerial surveys were conducted annually (except in 1997). Aerial surveys indicated a local beetle infestation at Bull Mountain (central British Columbia) during the 1960s, as well as a significant increase in the radial growth of lodgepole pine. The aerial survey data indicated a major mountain pine beetle outbreak beginning in the mid-1970s (Figure 7). Among the stands we sampled, this outbreak was first recorded near Canal Flats in southeastern British Columbia and then in the Cariboo-Chilcotin Plateau of central British Columbia. Although the outbreak crashed in these regions from 1984 to 1986, beetle infestations were recorded in many stands during the late 1980s and 1990s in southern British Columbia and Alberta (Figure 7). The substantial growth increases in lodgepole pine and Douglas-fir found in Canal Flats from the early 1970s to the mid-1980s are likely in response to stand thinning caused by beetle outbreaks. Among the 32 stands sampled in Cariboo-Chilcotin Plateau, we found that 27 had lodgepole pine growth releases that corresponded to detections of beetle infestations in aerial surveys (Figure 4) (Campbell et al. 2007). Two stands had no growth releases (No.109 and 120) and infestations were not detected in aerial surveys. Only three stands (<10%) produced contradictory information about the occurrence of beetle infestations. In stands 163 and 113, aerial surveys indicated an outbreak for which we found no corresponding growth release. In stand 107, we found a release in radial growth but no information indicating an outbreak in the aerial survey data. Radial growth releases corresponded similarly well with aerial survey data of beetle outbreaks in southern British Columbia during the late 1980s and 1990s (Figures 4, 5, and 7).

Recent aerial survey data indicated that mountain pine beetle outbreaks are currently occurring in the northernmost stands we sampled (Figure 7). Only the Doig Rd stand was infested during the 1970s/1980s outbreak. We detected no growth release among these northernmost stands, except for one in the Prince George stand during the late 1970s, two smaller releases from 1930 to 1940 in the Prince George stand, and another in Tweedsmuir Provincial Park. Both the tree-ring data and aerial survey data indicate that beetle outbreaks are expanding northward into areas where beetles probably could not persist previously.

Figure 4. Lodgepole pine growth release periods attributed to mountain pine beetle outbreaks in 85 stands over British Columbia and Alberta.

Note: Stands are arranged along a latitudinal gradient, with those at the top of the graph being the most northern stands sampled. x = 1st year of chronology with minimum 3 trees sampled. Gaps in Prince George chronologies represent undatable portions of the tree-ring series.
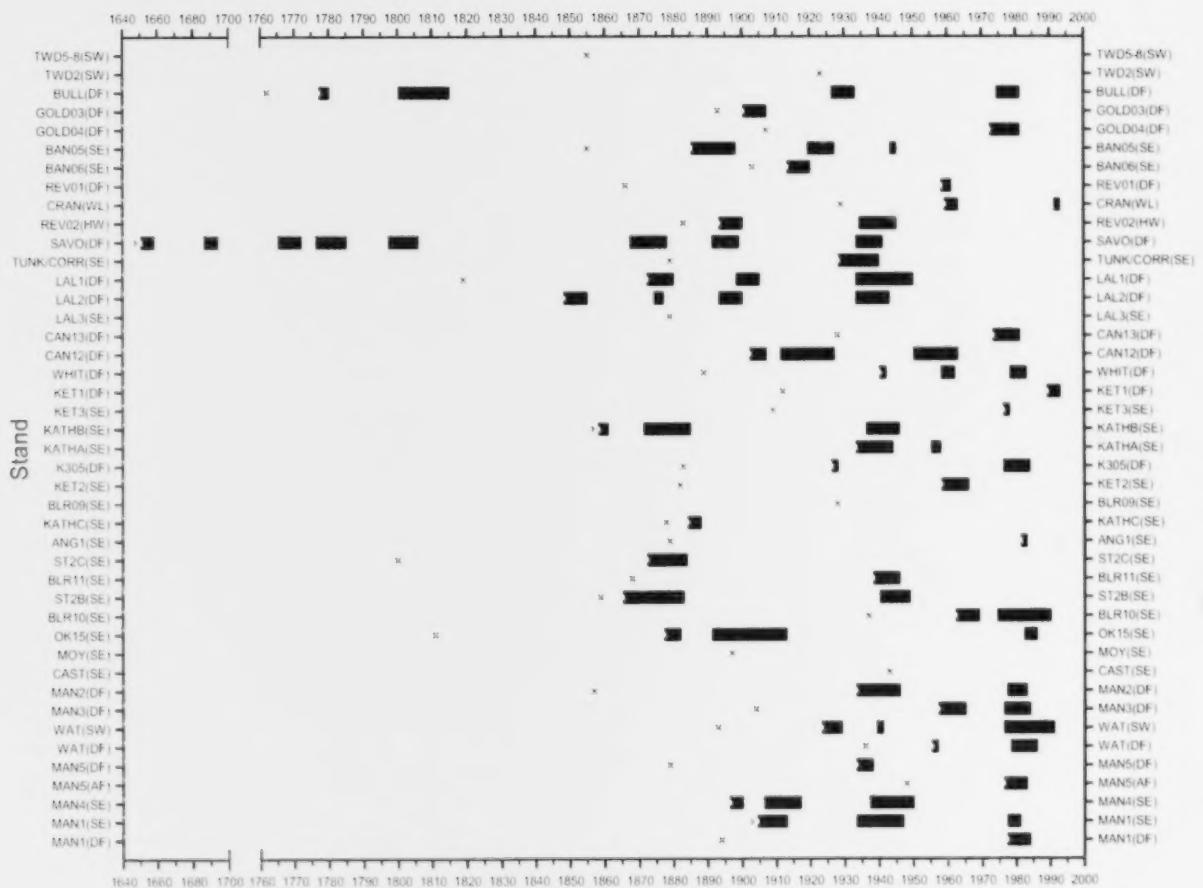
Figure 5. Non-host growth release periods attributed to mountain pine beetle outbreaks in 85 stands over British Columbia and Alberta

Note: Stands are arranged along a latitudinal gradient, with those at the top of the graph being the most northern stands sampled. Non-host trees included: Douglas-fir (DF), Engelmann spruce (SE), white spruce (SW), western hemlock (HW), western larch (LW) and subalpine fir (AF). Stands are arranged along a latitudinal gradient, with those at the top of the graph being the most northern stands sampled. x = 1st year of chronology with minimum 3 trees sampled.
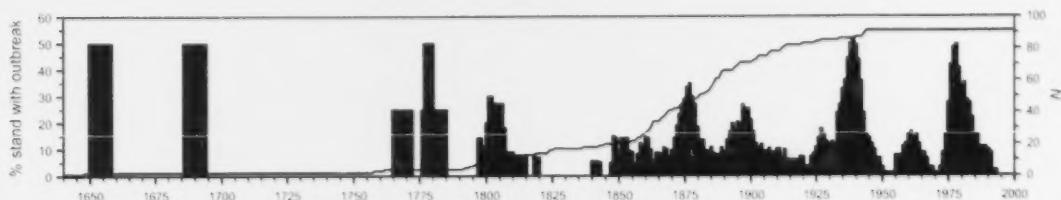
Figure 6. Annual frequency of stand-wide growth releases over the last 250 years (growth release data from lodgepole pine and non-hosts are combined).

Note: N = number of stands with tree ring data.

FIDS
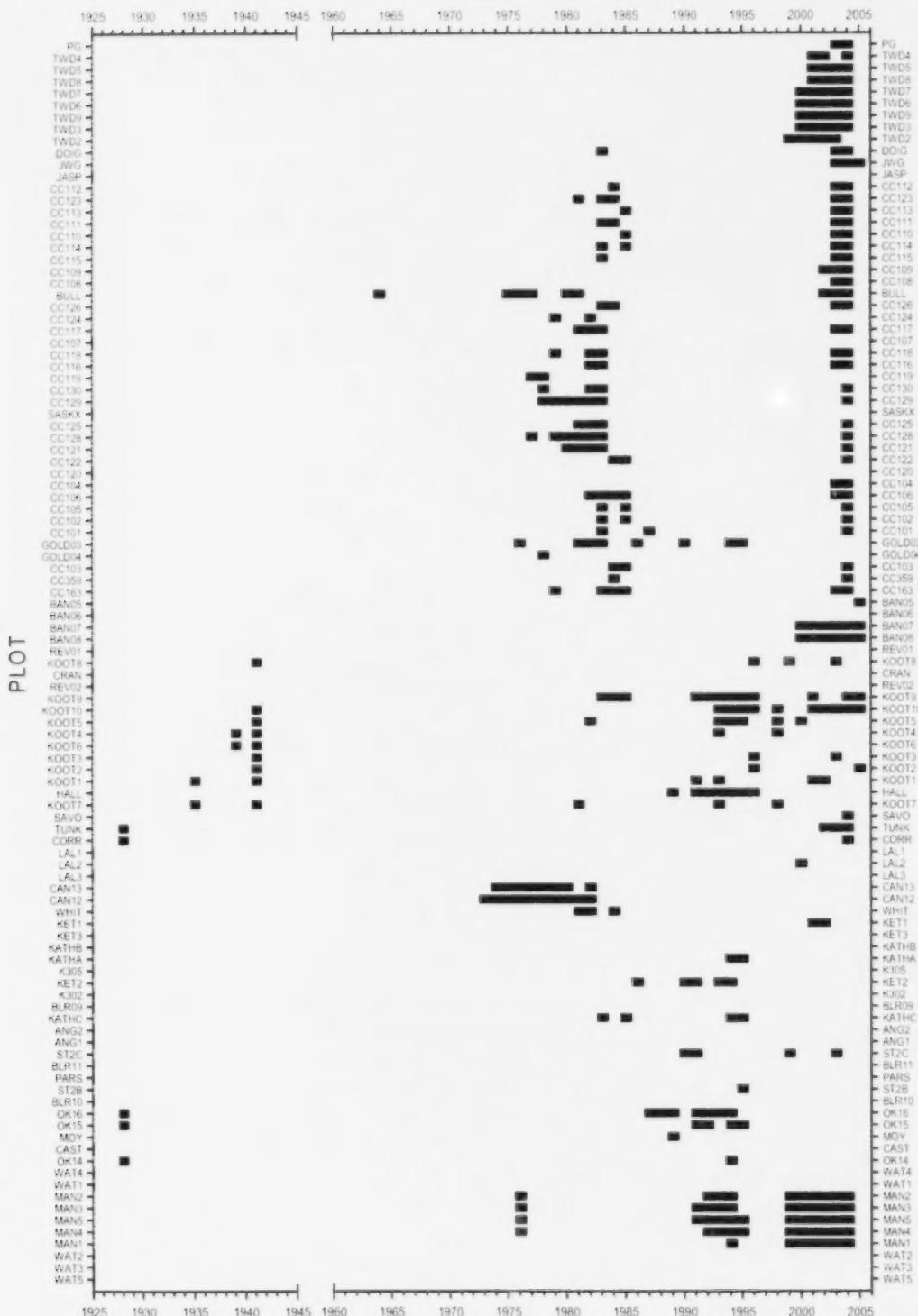
PLOT
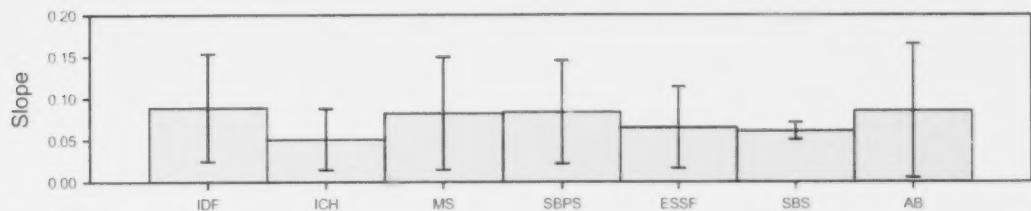
Figure 8. Intensity of mountain pine beetle outbreaks (as indicated by the slope of the increasing portion of a growth release) by biogeoclimatic zone.
Note: AB = Alberta, ESSF = Engelmann Spruce-Subalpine Fir zone, ICH = Interior Cedar-Hemlock zone, IDF = Interior Douglas-fir, MS = Montane Spruce, SBPS = Sub-Boreal Pine – Spruce, SBS = Sub-Boreal Spruce.

3.2.1.1   Pine death dates

Death dates of beetle-killed trees sampled in the Cariboo-Chilcotin Plateau were summarized graphically (Figure 9) and as vertical bar graphs on the master tree-ring chronologies produced for each stand. Over the entire region, tree death dates indicate a beetle outbreak during the 1970s and 1980s (Figure 9). The number of trees killed by beetle peaked in 1983 and 1984. For all master chronologies that extended beyond 1987, we observed substantial increases in mean tree growth of surviving trees that corresponded with the death dates of beetle-killed trees.

3.2.1.2   Dated beetle scars

Beetle scars peaked around 1905, 1932, and 1982 in the Cariboo-Chilcotin Plateau (Figure 10). The 1982 peak is associated with the well-documented outbreak of the 1970s and 1980s. The 1932 peak occurred during substantial host growth releases and probably corresponds to an outbreak. In stand 104, six beetle scars on sampled trees date to 1906. Although some stands in this region had growth releases that indicate a beetle outbreak at that time, stand 104 did not.

3.3   Climate, tree growth, and beetle outbreaks

3.3.1   Weather associated with past beetle outbreaks in British Columbia and Alberta

Aerial surveys detected attacked trees (red in colour) in the Cariboo-Chilcotin Plateau of central British Columbia from about 1974 to 1986 (Figure 7). Beetle-infested trees generally turn red and die in the year following mass-attack. This means that mass attacks by beetles probably occurred between 1972 and 1973. At least 20% of the trees we sampled in this region had a pulse of increased tree growth between 1975 and 1979, with the percentage of lodgepole pine trees showing a doubling of growth peaking between 1976-1978, two to four years after the first dead trees were observed there (Figure 11a). Although mean annual temperatures hovered around the average, warmer-than-average summer temperatures occurred from 1969-1972 (Figure 11a). These warmer summer temperatures were accompanied by drought (i.e., high aridity indices) in 1970 and 1971 (Figure 11a), which occurred again in 1973 and 1974 (Figure 11a); 1970 and 1974 are among the driest on record for this region. Tree drought stress may have contributed to the initiation of the outbreak that began in the mid-1970s. Local knowledge, as well as other

documentary and dendrochronological evidence, indicate beetles infested the region between 1928 and 1942 (L. Safranyik, D. Linton, *pers. comm.*). We observed a pulse in radial tree growth from about 1930 to 1944, with the frequency of trees in release peaking between 1937 and 1941. An 8-year period of warmer-than-average summer temperatures from 1922 to 1929 was accompanied by high drought indices. A period of moist, warm conditions starting in 1939 was associated with higher-than-average tree growth until about 1950. Although weather can be a confounding influence to identifying outbreaks from tree growth releases, this warm, moist trend occurred mostly after the peak of tree growth releases, suggesting that factors other than climate were influencing growth. We presumed this other factor to be a beetle outbreak.

All Stands (101-130)
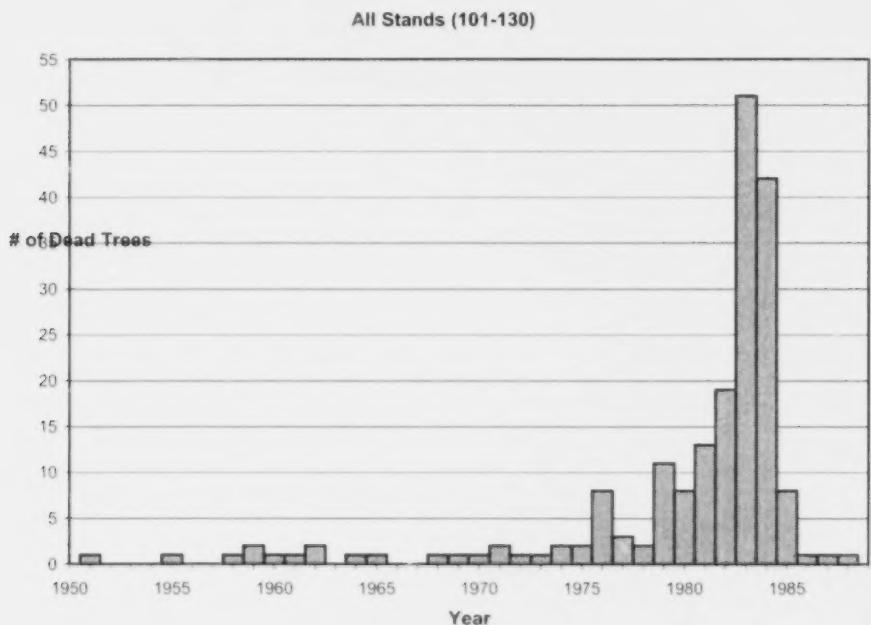
Figure 9. Number of beetle-killed lodgepole pine trees per year during the last mountain pine beetle outbreak in the Cariboo-Chilcotin Plateau of central British Columbia.
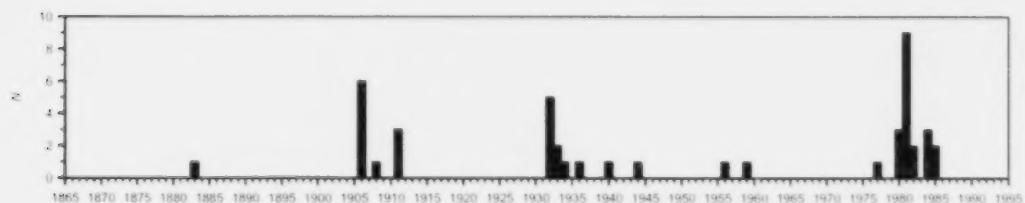
Figure 10. Number of beetle scars per year found on disks collected from lodgepole pine in the Cariboo-Chilcotin Plateau of central British Columbia.

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The available aerial survey data available did not indicate any mountain pine beetle outbreaks in Banff National Park until 1999 (Figure 7). However, other documentary records for the park indicated that small isolated outbreaks occurred during the 1940s and the 1980s. This coincides with major beetle outbreaks documented (through aerial surveys) on the other side of the continental divide in Kootenay National Park in 1935 to 1941 and from 1980 onwards (Figure 7). We observed four periods of increased radial tree growth from the available instrumental weather data: 1895-1910, 1938-1944, 1954-1964, and 1968-1989 (Figure 11b). Peaks in growth release occurred from 1956 to 1958 and from about 1978 to 1984. There was a 5-year period (1969-1973) of warmer than average summers in the park prior to the 1978 to 1984 peak in growth releases. After the peak, however, an unprecedented period of warm, moist summers was not associated with major growth releases, suggesting that this peak in growth release may have been due to stand thinning by beetle rather than climate. No beetle outbreaks were documented in the park during the growth releases observed from 1954 to 1964, but a drought occurred during this time, with the second driest year on record occurring in 1956. This level of drought is within the range observed before the start of the current outbreak in 1999.

Shifts in the Pacific Decadal Oscillation (actual measured data and values reconstructed from tree-rings) were compared to annual monthly and seasonal fluctuations in temperature and precipitation (Figure 12). Both the Cariboo-Chilcotin Plateau and Banff National Park had significant positive relationships between fluctuations in mean annual temperature and the measured PDO values (Table A4, Figure 12). The positive relationships between mean annual temperatures and PDO were largely due to high correlations with temperatures from October to May (Table A4, Figure 12). So, when sea surface temperatures warmed during these months, so did the continental climate in these regions. Both the 1940s and 1980s mountain pine beetle outbreaks occurred when the PDO was in a positive phase and temperatures were warmer (Figure 12). Cold temperatures from October to May can drastically reduce beetle populations (Safranyik and Carroll 2006). Extreme cold temperatures occurred during these months in 1948 to 1951 and in 1954 to 1955, when the PDO shifted to a negative phase from about 1948 to 1956 and probably contributed to the collapse of the 1940s beetle outbreak. The PDO shifted into a positive phase between 1977 and 1976. In Banff National Park, this shift was associated with long periods of warm temperatures in March and April (Figure 12b), and probably facilitated the development of the current outbreak in the park. The PDO was positively correlated with precipitation in September in the Cariboo-Chilcotin Plateau (Figure 12a), but negatively correlated with winter precipitation in Banff National Park (Figure 12b). Snowmelt may contribute significantly to growing season moisture content. In Banff National Park, however, a decrease in winter precipitation was not associated with growing season drought because mean summer precipitation during this period was above average.
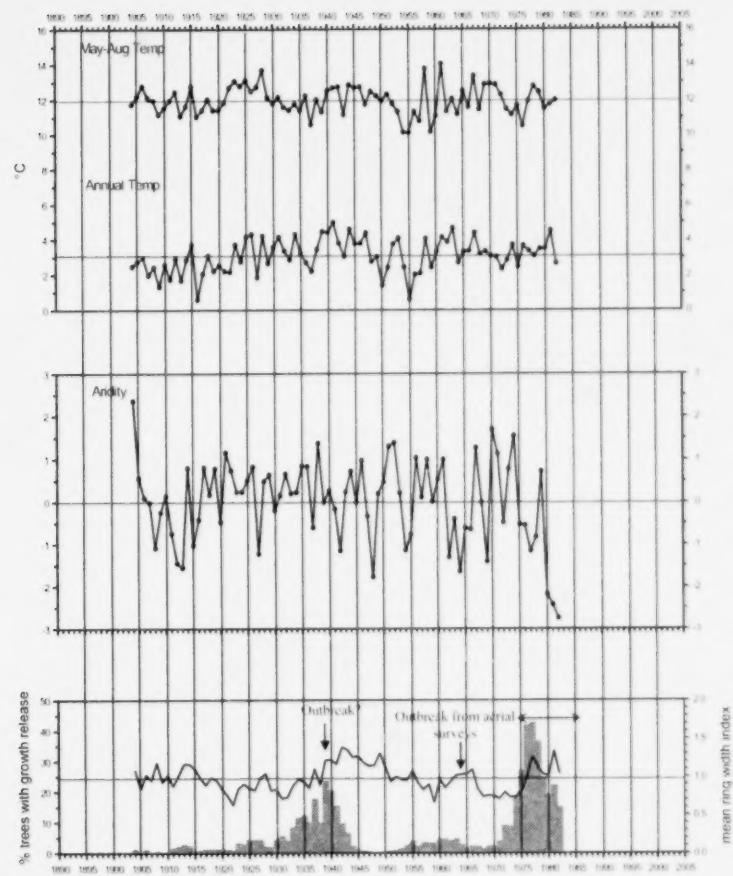
a) Cariboo-Chilcotin, British Columbia
b) Banff National Park, Alberta
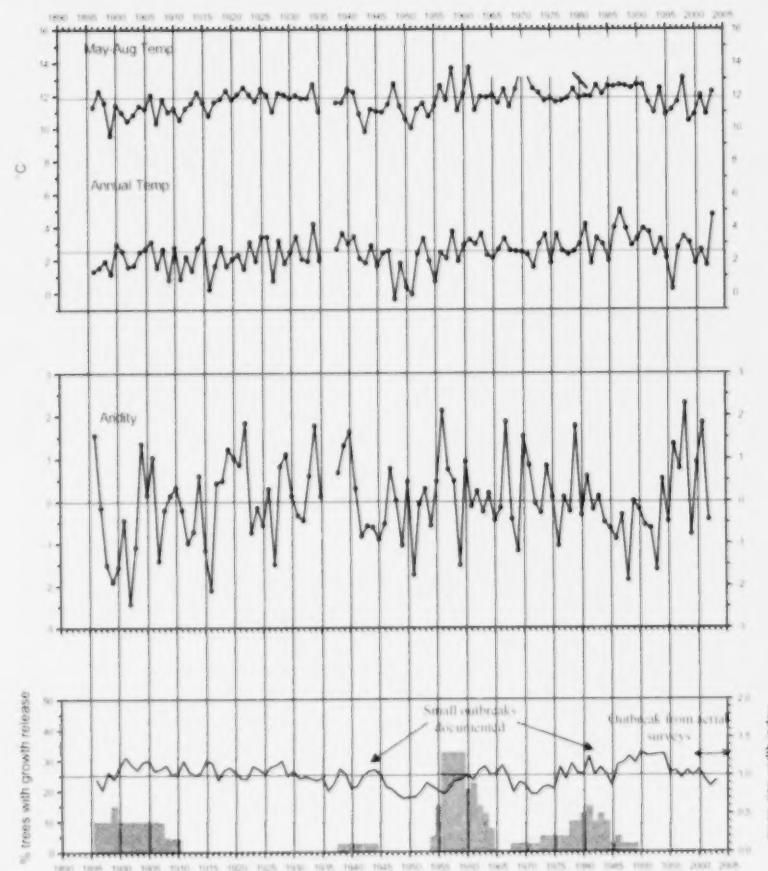
Figure 11. Relationships between mountain pine beetle outbreaks and mean annual temperature, mean summer temperature (May-August) and an annual aridity for stands sampled in central British Columbia (Cariboo-Chilcotin) and Alberta (Banff National Park).

Note: Beetle outbreaks were identified through the detection of radial growth releases (at least 25% increase in growth) among surviving trees and from aerial surveys or documentary records of these regions.

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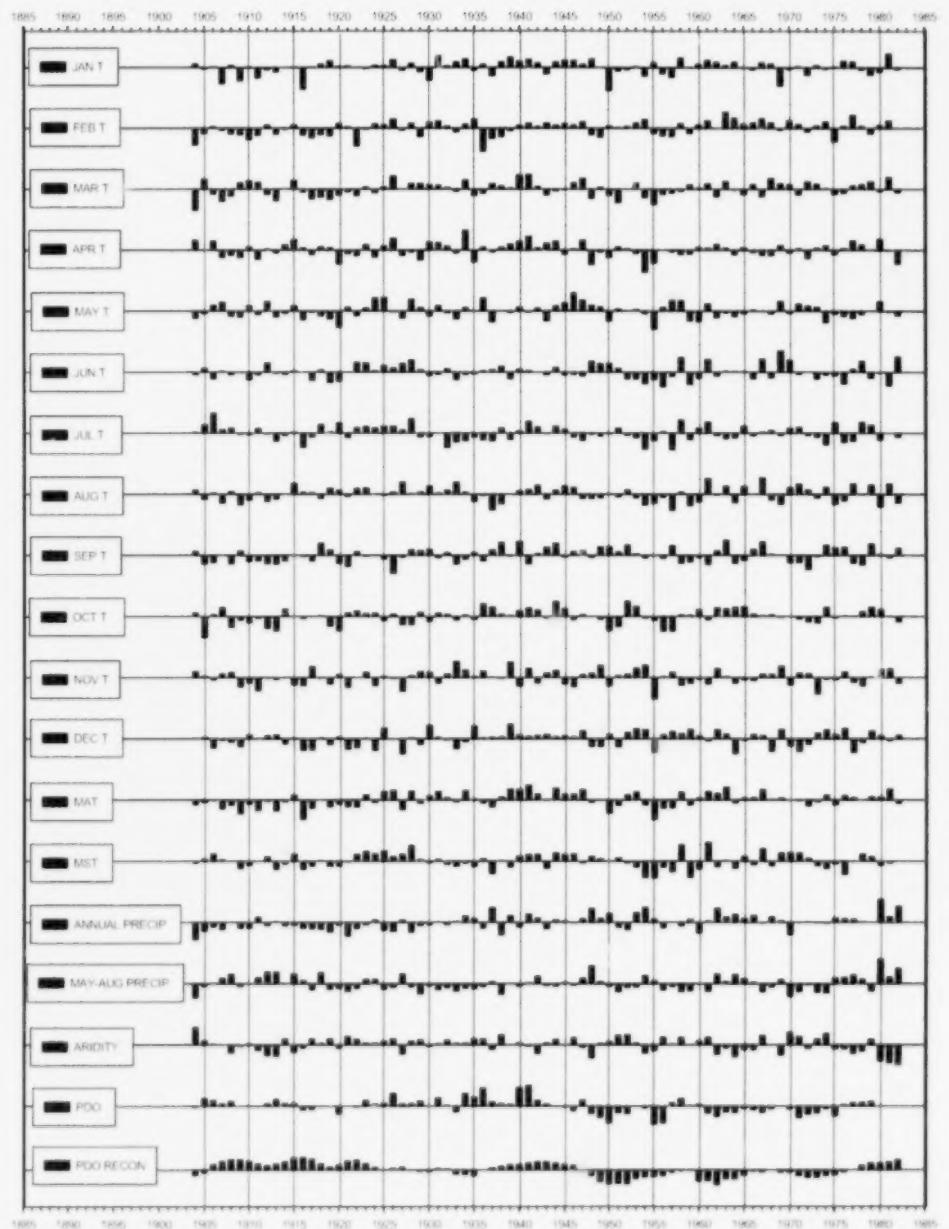
a) Cariboo-Chilcotin

Figure 12. Monthly, seasonal and annual variations in instrumental weather data for the Cariboo-Chilcotin Plateau in central British Columbia and Banff National Park.
Note: An aridity index was derived from monthly temperature and precipitation. Variability in weather data was compared to the Pacific Decadal Oscillation (PDO, measured and reconstructed values). All data were standardized.

Figure 12 (cont).
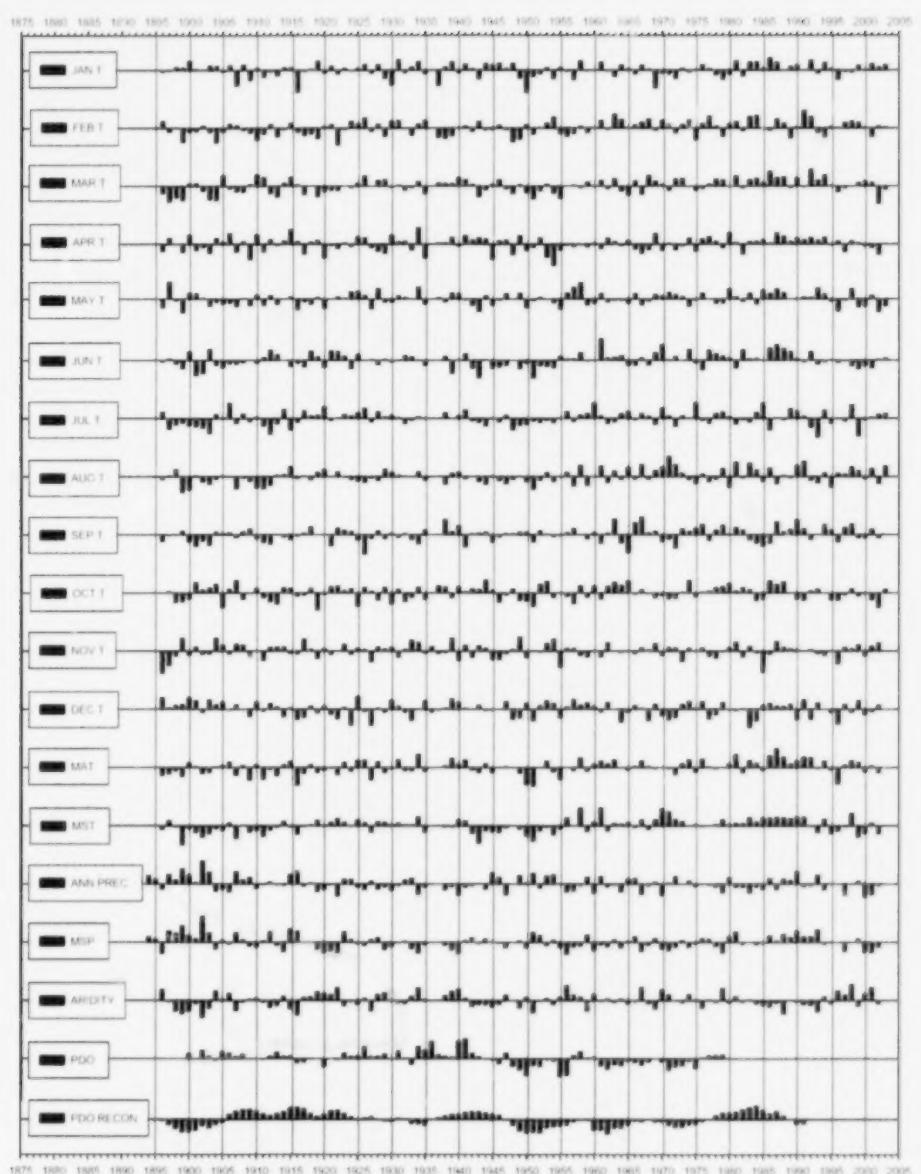
b) Banff National Park

Neither the standardized nor residual chronologies of tree-ring widths of lodgepole pine and Douglas-fir in the Cariboo-Chilcotin Plateau correlated to the PDO, suggesting that tree-ring patterns might be influenced more by local site conditions or stand history (e.g., forest disturbances) than by regional climate. In Banff National Park, however, the standardized chronology of tree-ring widths for lodgepole pine was significantly related to fluctuations in the PDO, suggesting climate may have had a stronger influence than local site conditions or stand history.

3.3.2 Effects of temperature and precipitation on tree growth

Mean standardized chronologies of indexed tree-ring widths for lodgepole pine and Douglas-fir were generated for the entire tree-ring record (Figure 13). Relationships between temperature, precipitation, and radial growth were analysed for the periods when instrumental climate records were available (n = 78 years for the Cariboo-Chilcotin Plateau and n = 107 years for Banff National Park). Response function analyses indicated that 53% to 65% of the variation in lodgepole pine and Douglas-fir tree-ring widths over the last century could be attributed to fluctuations in temperature and precipitation (Figure 14).

Tree-ring widths of lodgepole pine and Douglas-fir in the Cariboo-Chilcotin Plateau were sensitive to current growing season precipitation (May, June, and July), with better growth occurring in years with more rainfall (Figure 13a). Current year growth was also positively related to precipitation in the previous August, likely because late-summer and fall precipitation can be stored in the soil for use in the following spring. There was a significant positive relationship between lodgepole pine ring width and fall/winter temperatures (October, November, and January; Figure 14a). This is presumably because warmer temperatures, particularly in the fall, extend the growing season. Douglas-fir growth was negatively related to growing season temperatures in the current and previous year (Figure 13a). The negative effect of high growing season temperatures on Douglas-fir growth was stronger than that on lodgepole pine, probably because these trees occurred on steep, rocky slopes and were more sensitive to drought when temperatures were high.

Tree growth responses to temperature and precipitation in Banff National Park were similar to those in the Cariboo-Chilcotin Plateau. Higher precipitation in the previous autumn and during the summer was strongly correlated with increased radial growth of lodgepole pine and Douglas-fir. High temperatures in the spring and fall of the current year were also significantly correlated with increased radial growth of these species, probably because they increased growing season length. But high temperatures in the previous fall had a negative effect on growth, perhaps because high fall temperatures can decrease the amount of water stored in the soil over the winter and thus decrease the amount available to trees in the spring. Although the current year of Douglas-fir growth was negatively affected by high summer temperatures, the growth of lodgepole pine was not. This may be because Douglas-fir on the steeper, rocky slopes are more sensitive to drought stress when temperatures are high.
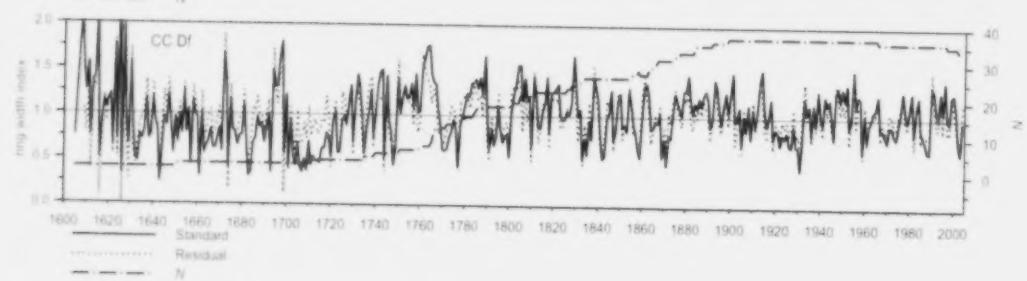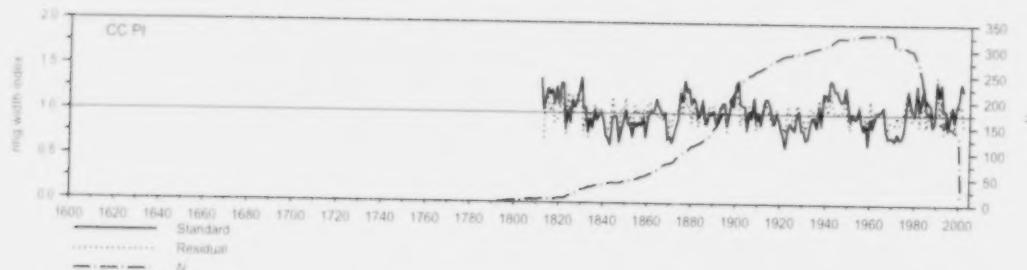
a) Cariboo-Chilcotin Plateau
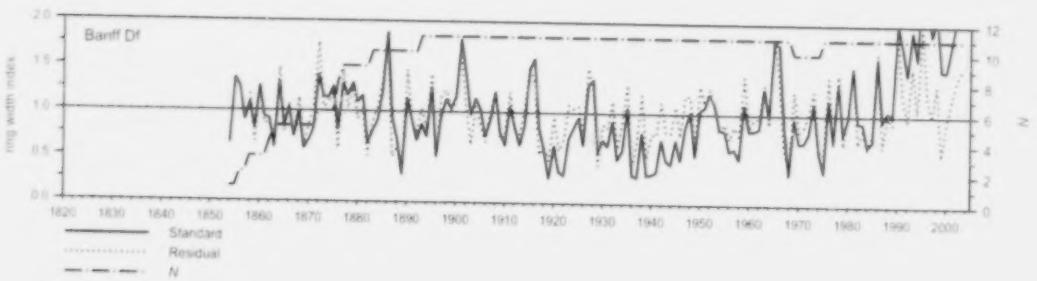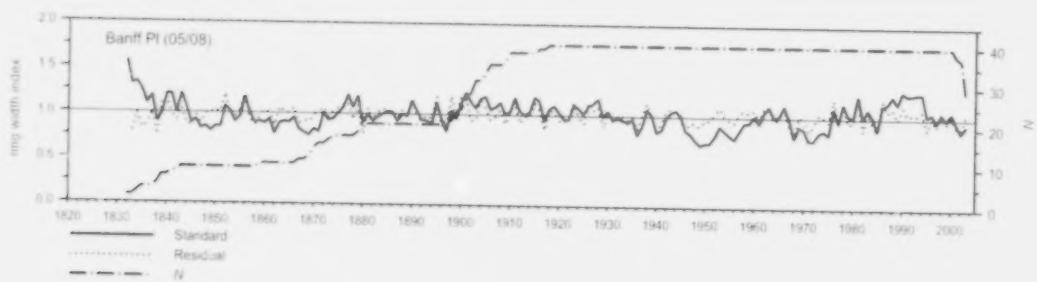
b) Banff National Park

Figure 13. Standard and residual chronologies of tree-ring widths for lodgepole pine and Douglas-fir in the Cariboo-Chilcotin Plateau, British Columbia, and Banff National Park, Alberta.

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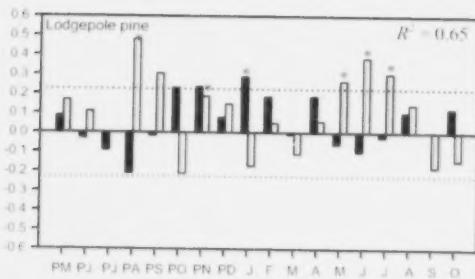
a) Cariboo-Chilcotin Plateau, British Columbia
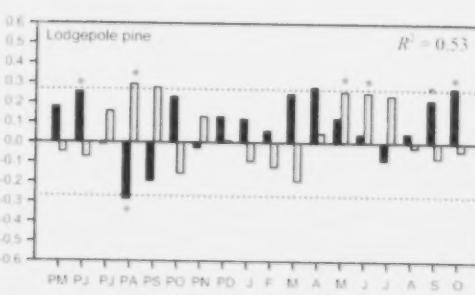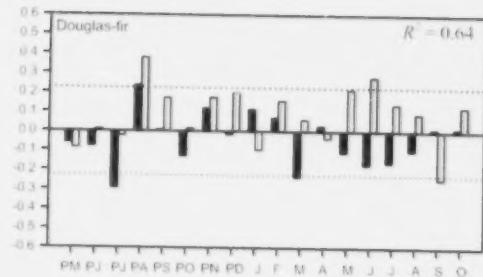
b) Banff National Park, Alberta:

Temperature (°C) – ▉
Precipitation (mm) – ☐
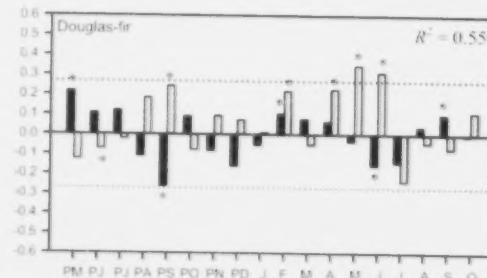
Figure 14. Pearson correlations and bootstrapped response function analyses used to assess relationships between tree–ring width and a monthly index of aridity (May to October) for the Cariboo-Chilcotin Plateau, British Columbia, and Banff National Park, Alberta.

Note: The dotted line indicates significant Pearson correlations and the asterisk (*) indicates significant results using response function analysis.
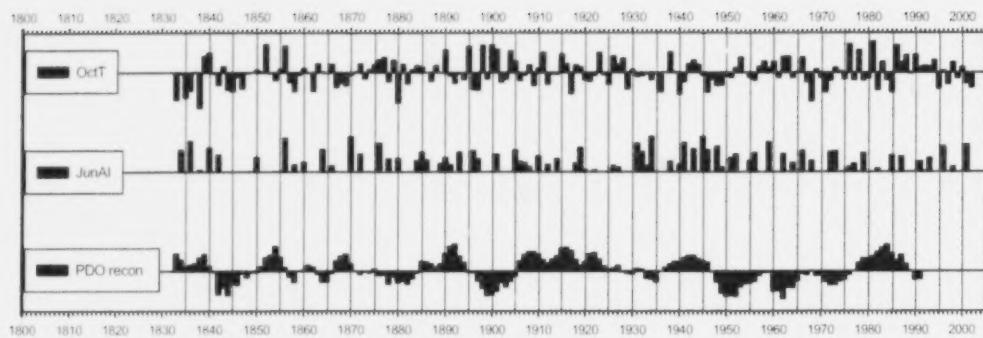
a) Banff National Park, AB
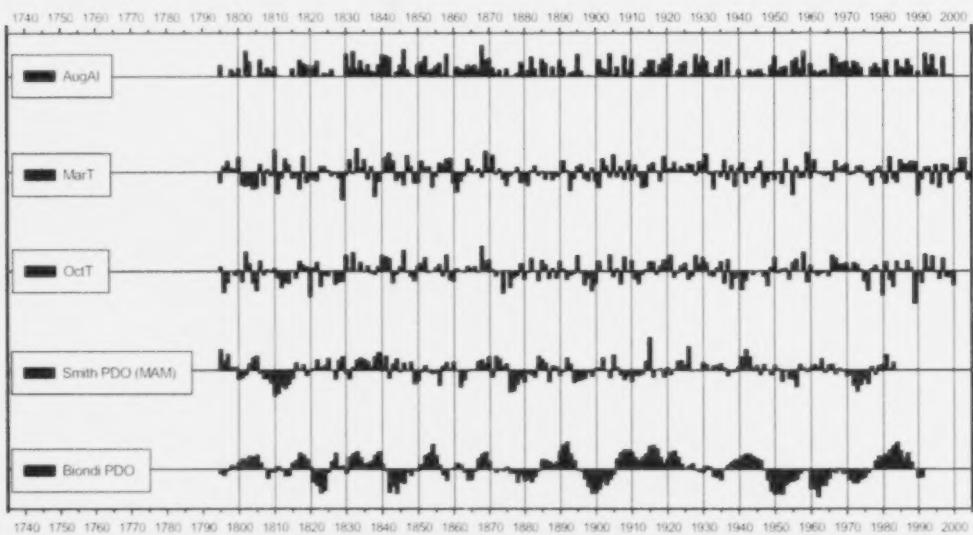
b) Cariboo-Chilcotin, BC

Figure 15. Tree-ring reconstructions of selected climate variables for Banff National Park (mean October temperature and a June aridity index) and the Cariboo-Chilcotin Plateau (mean March and October temperatures, and an August aridity index).
Note: Comparisons were made with tree-ring reconstructions of the Pacific Decadal Oscillation (PDO) of sea surface temperatures. PDO (MAM) are reconstructions for March, April, and May sea surface temperatures only.

PRECON was also used to test for relationships between tree-ring width and a growing season (May to October) aridity index derived from temperature and precipitation data. The aridity index explained much less of the variation in annual tree-ring widths than either temperature or precipitation alone ($R^2 = 0.10$ to 0.244) (Figure 14a). In the Cariboo-Chilcotin Plateau, drought in October had a significant negative effect on tree growth. The highest correlation coefficients between Douglas-fir ring widths also occurred in October but were of borderline statistical significance. The lodgepole pine sampled in Banff National Park were much more sensitive to drought than those in the Cariboo-Chilcotin Plateau (Figure 14b). But, like the Cariboo-Chilcotin Plateau, there was a negative effect between ring width and drought in the fall (in the previous and current year). Drought in May of the current year had a significant negative effect on the growth of Douglas-fir.

3.3.3 Tree-ring reconstruction of historical climate over the last two centuries in central British Columbia and Alberta

From lodgepole pine and Douglas-fir increment cores collected in Banff National Park, we reconstructed a mean October temperature index and an aridity index for June (Figure 15a). Historical reconstructions extended back to 1833. Model predictions correlated well with data reserved to test models ($p < 0.10$). Since 1833, we found a distinct increase in the number of years with arid Junes. Lower-than-average October temperatures (> 1 standard deviation) were 10% more common prior to 1900. Reconstructed October temperatures were not significantly correlated with the Pacific decadal reconstruction of Biondi et al. (2005).

August aridity and March and October temperatures were reconstructed from lodgepole pine and Douglas-fir tree-ring chronologies for the Cariboo-Chilcotin Plateau in central British Columbia (Figure 15b). Regression models correlated poorly with data values set aside to validate models. Further work to produce valid models in this region is necessary.

3.3.4 Model estimates of historical climate and predictions of future climate in British Columbia and Alberta

3.3.4.1 Climate conditions averaged over all stands

Historical and future climate conditions were summarized over all stands from which we collected tree-ring data. Historical conditions were estimated from interpolated instrumental weather data for the climate normal period 1961-1990 (i.e., 1975 climate period), and the climate model ClimateBC was used to predict future climate under a particular climate change scenario (i.e., CGCM2-A2x, available at http://genetics.forestry.ubc.ca/cfgc/climate-models.html). Mean annual temperature (MAT) during the 1975 climate period averaged -2.6 °C and model prediction indicated an increase to -1.3, -0.2, and 1.4 °C in the 2020s, 2050s, and 2080s, respectively. Other annual variables related to temperature (e.g., chilling degree days, frost free period and extreme minimum temperature) showed similar trends. Mean annual precipitation (MAP), mean summer precipitation (MSP), and mean precipitation as snow (PAS) averaged 648 mm, 269 mm and 383 mm, respectively, over all stands. Model predictions indicated little change in MAP or MSP from 1975 to the 2080s over sampled stands, but PAS decreased slightly. As expected given a rise in temperature with no increase in precipitation, stand aridity (i.e., AHM and SHM) increased significantly from 1975 to the 2080s.

Cold temperatures in the winter, spring, and fall can cause significant beetle mortality (Safranyik and Carroll 2006). Average observed temperatures over all stands were -11.9°C (min -15.2°C, max -2.8°C), -3.5°C (min -8.6°C, max 7.9°C), and -2.0°C (min -6.9°C, max 7.7°C) in the winter, spring, and fall, respectively. The model predicted a 4.2°C, 5.2°C, and 2.9°C increase in winter, spring, summer and fall temperatures from 1975 to the 2080s. Model predictions indicated that

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the largest increase in temperatures (i.e., 5.2°C to 5.9 °C) from 1975 to the 2080s will occur during February, March, and April. This finding suggests that increasingly favorable spring temperatures will likely have the greatest influence on beetle population densities.

3.3.4.2   *Climate conditions averaged over biogeoclimatic zone*

Historical climate and future climate conditions were also summarized for each biogeoclimatic zone in which we sampled stands. The coldest climate occurred in the high-elevation ESSF (dc and dm subzones) and MS (xk and xv subzones) zones. Mean Annual Temperature were <-4.0 from 1961 to 1990. Model predictions indicated 4.0°C and 3.7°C increase in MAT from 1975 to the 2080s. Mean Annual Temperature in all other zones had a similar increase (i.e., 3.6°C to 4.5°C), as did winter and spring temperatures.

The IDF zone (dm and dk subzones) has the driest climate: the aridity indices (AHM and SHM) were much higher in this zone than in any other (i.e., 83.5 in the dk subzone and 49.2 in the dm subzone, respectively). Model predictions indicated more substantial increases in the aridity index of this zone than in any other biogeoclimatic zone.

3.3.4.3   *Climate conditions in selected stands*

Historical climate conditions and future climate were summarized for stands where outbreaks had occurred at least 150 years ago (stands 128 and 130 of the Cariboo-Chilcotin Plateau) and in stands where outbreaks had occurred more recently. Mean Annual Temperature from 1961 to 1990 was lowest (-5.5°C) in Banff National Park, as were the extreme cold temperatures. Model predictions indicated that MAT increased the most in Banff National Park, to 4.3°C by the 2080s. Increases in MAT temperature were similar for other stands (i.e., 3.2°C Prince George stand, and 3.6°C and 3.7°C for stands 128 and 130 in the Cariboo-Chilcotin Plateau).

As with data summarized for all stands, increases in temperature were greatest among the spring months, particularly February, March, and April.

Stand 130 of the Cariboo-Chilcotin Plateau had the most arid conditions (SHM = 62.50). This was followed by stand 128 in the Cariboo-Chilcotin Plateau (SHM = 47.6), the Prince George stand (SHM = 25.4) and the Banff National Park stand (SHM = 10.7). Model predictions indicate that aridity indices for stands in the Cariboo-Chilcotin Plateau in central British Columbia will increase much more than those in either Prince George or Banff National Park.

3.4   Mountain pine beetle outbreaks and fire history

3.4.1   The history of low intensity surface fires in central British Columbia

Sixty-one fire scars were dated on disks collected from trees in the Cariboo-Chilcotin Plateau. Most fires occurred before 1900 (Figure 16); fire disturbances peaked in 1830, 1890, and 1910. The 1890 and 1910 peaks coincide with growth releases attributable to beetle outbreaks. Although it is possible that surface fires generated a growth release, it is more likely that growth releases represent beetle outbreaks and that a fire occurred as a result of increased fuel loads created by an outbreak.

By overlaying the dates of fire scars onto master chronologies of radial tree growth, we found that there was no consistent relationship between growth patterns and fire events. Although 33% of fire scars were associated with a growth release among mature trees, 14% were associated with a decrease in growth. There was no change in growth (an increase or decrease) associated with 28% of the fire scars. About 33% of the fire scars were associated with the early rapid growth of trees or occurred before the earliest year of our master chronologies. Fire scars dated to these times probably generated the lodgepole pine cohort from which we collected most of our tree-ring data.
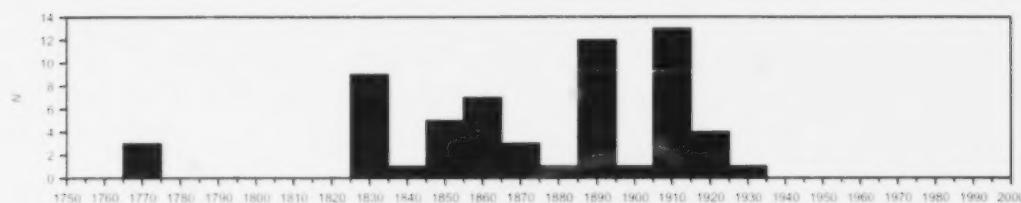
Figure 16. Number of fire scars per decade in the Cariboo-Chilcotin Plateau, Central British Columbia.

3.4.2 Relationships between beetle outbreak occurrence and fire severity and frequency

Based on growth release data for each stand sampled, we determined whether a beetle outbreak occurred during the 1930s/1940s outbreak and the 1970s/1980s outbreak. For each stand we also assigned a fire frequency and fire severity class (Tables A5 and A6). Outbreak occurrence data from both outbreak periods were pooled and the frequency of stands (%) with beetle outbreaks was calculated for each fire severity and fire frequency class. We found that the outbreak frequency was nearly the same for all three fire frequency classes: 36%, 26%, and 33%. However, outbreaks were more frequent among low severity and mixed severity fire regimes, 36% and 33% respectively, than among stands where fires tended to be stand-replacing (24%).

3.4.3 Probability of beetle outbreaks as a function to time since last stand-replacing fire

Outbreak frequency was determined by pulses of lodgepole pine and was tabulated for four periods representing time since last stand-replacing fire: 10-50 years, 60-100 years, 110 to 150 years, and >150 years. Once again, outbreak data from both the 1930s/1940s and 1970s/1980s outbreaks were pooled. Outbreaks were rarest among stands initiated by a recent fire (i.e., 10-50 years ago) (Table A7) and most frequent among stands initiated by fire more than 150 years ago (Table A7), but the sample size for this category was small ($n = 4$), making this data difficult to interpret. Although stands initiated between 60-100 years ago also had relatively 1 outbreaks, outbreaks in stands initiated between 110-150 were less frequent (Table A7).

4 Discussion

4.1 Reconstruction of beetle outbreaks from tree-ring data

Heath and Alfaro (1990) attributed synchronous increases in the radial growth of trees at Bull Mountain, British Columbia to stand thinning caused by lodgepole pine deaths during mountain pine beetle outbreaks. The present project built on these initial findings and used tree-ring data collected throughout British Columbia and Alberta to identify pulses of increased growth to reconstruct the history of beetle outbreaks over the last two centuries. Because some lodgepole pine survive beetle outbreaks, tree-ring data from both surviving hosts and non-hosts were used. The study was designed to ensure that sampling covered the entire range of the current outbreak (based on aerial survey data for 2003), so that we could examine the history of outbreaks in areas where outbreaks are thought to have a long history (e.g., central British Columbia) and in areas where they are thought to be more recent (e.g., near Prince George and in Alberta).

Mountain pine beetle outbreaks were reconstructed from growth release data obtained from 85 of the 121 stands from which samples were collected. Poor quality samples, difficult to cross-date

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tree-ring data, and small sample sizes resulted in the elimination of tree-ring data from 36 stands. Nevertheless, data from the remaining 85 stands permitted us to develop a history of outbreaks over the current geographic range of beetle outbreaks and over a time scale of least 150 years. To our knowledge, no other tree-ring database exists that can be used to reconstruct beetle outbreaks for such a large area.

The use of dendrochronological methods to detect past mountain beetle outbreaks rests on the premise that significant growth releases occur among surviving trees. First, we removed subjectivity of identifying growth releases visually by automating the process using the dendrochronology program JOLTS. The JOLTS program was then run three times on individual trees of each stand to detect: at least 25% increases in growth; at least 50% increases in growth; and at least 100% increases in radial growth. Frequency graphs showing the number of trees releasing in each year were produced and an outbreak was considered to occur in a stand when at least 30% of the trees had synchronous increases in growth that lasted at least 3 years. We compared the results with various corroborating evidence of beetle infestations for the last beetle outbreak of the 1970s and 1980s (i.e., aerial surveys identifying beetle outbreaks, death dates of beetle-killed trees and dated beetle scars). We found that runs of JOLTS using growth release sensitivity of at least 25%, along with the 30% criterion of trees releasing, was best able to identify beetle outbreaks. By including trees with releases of 25% to 50%, it is likely that we included some that were not caused by beetle outbreaks. But by using a growth release sensitivity of at least 50%, we missed many documented outbreaks of the 1970s/1980s, and using the 100% growth release sensitivity, we missed most documented outbreaks. Although a few studies on spruce bark beetles have relied on a doubling of growth to identify beetle outbreaks (e.g., Veblen et al. 1991 a,b), we did not find that it worked very well in this study, given that we also required at least 30% of trees in a stand to show a release to identify a stand-wide disturbance. A possible reason for this is that we tested our ability to detect outbreaks using tree-ring data and documentary evidence of the 1970s/1980s, when many of the trees we sampled were already mature (i.e., 60-80 years old). Although the collection of increment cores and disks from old trees was necessary to obtain tree-ring chronologies that spanned at least 100 years, tree age or size could affect our ability to detect recent outbreaks if very large growth increases (e.g., a doubling in radial growth) were set as a criterion for identifying outbreaks. Earlier work indicates that small, young trees, typically those growing in the understorey, tend to have larger increases in radial growth following outbreaks than mature trees simply because of their size (Heath and Alfaro 1990). We feel, therefore, that the criteria we set for identifying outbreaks from tree-ring data (i.e., at least a 25% increase in growth over 30% of trees in a stand) represents a reasonable compromise between including some releases that were not outbreaks and missing recent outbreaks that could be identified in older trees. Moreover, even with the 25% cut-off point, mean growth releases over all stands and all release periods was 65% for hosts and 58% for non-hosts, far above the minimum 25% criterion set for identifying releases.

Pulses of growth release among trees that survive beetle outbreaks are the chief source of evidence for historical beetle outbreaks for periods before aerial surveys or other documentary evidence and can be used to identify beetle-killed trees and outbreaks. Within the long-term record of growth releases, there are other potential causes of canopy thinning besides mountain pine beetle including logging, fire, diseases, other insects, and blowdown. We made a concerted effort to exclude stands in which we found any evidence of more recent logging activity (e.g., cut stumps) in order to remove the likelihood that logging after 1900 might account for growth releases. Fires, especially low-intensity surface fires, could thin stands or alter soil growing conditions and cause a synchronous increase in tree growth within a stand. However, fire scar data obtained from trees in central British Columbia showed that fires did not occur in these

stands after 1910 and thus could not account for growth releases attributed to the beetle after this date. Prior to 1910, we found that fire scars were not consistently associated with growth releases (many were associated with decreases or no change in growth). Even if fire scars were dated to a growth release period, many other stands had concurrent growth release periods without any evidence of fire. We suspect that growth releases coincident with fire scars were more likely due to increased fuel loads caused by a beetle outbreak. Outside the Cariboo-Chilcotin Plateau, germination dates of lodgepole pine indicated that fire was a stand-replacing disturbance and left few survivors. Diseases and other insect outbreaks are potential alternative hypotheses for explaining the growth release periods we documented in the tree-ring chronologies. However, no other disease generates the stand-thinning response that occurs synchronously among stands over vast areas (e.g., the spread of root-rots are slow and localized disturbance events which cause reduced growth of survivors). The pine engraver, *Ips pini*, could have stand-thinning effects similar to mountain pine beetle, but its outbreaks are likely to be more localized in space and time because they require lots of dead wood (from logging or blowdown) to build populations big enough to substantially damage lodgepole pine. Blowdowns could explain some of the releases we detected in stands, but is an improbable explanation for synchronous growth releases over large geographic areas.

Years of warm weather can cause synchronous periods of fast tree growth that could be mistaken for releases caused by beetle outbreaks. However, if warm weather is not accompanied by increased soil moisture, either through rain or snowmelt, resulting drought conditions are likely to reduce tree growth (see results section on radial tree growth and climate). For selected stands, we examined relationships between chronologies of radial growth and climate in more detail. We compared mean chronologies of radial growth (standardized and residual) with published values of the Pacific Decadal Oscillation (PDO), an indicator of large-scale climate shifts. We found that while the standardized chronology of lodgepole pine growth in Banff National Park was significantly correlated with the PDO, temporal patterns of tree growth in the Cariboo-Chilcotin Plateau were not. The significant increase in tree growth that we found during the 1950s in Banff National Park could be due to a decade of warm temperatures combined with increased precipitation and snowmelt (Watson and Luckman 2005a,b), as there is no evidence of beetle outbreaks in the park during this time. The Cariboo-Chilcotin Plateau had similar increases in temperature during the 1950s and 1960s, but no substantial increases in tree growth like those found in Banff National Park, possibly due to regional differences in topography and availability of snowmelt/runoff. In the Cariboo-Chilcotin Plateau region, documentary evidence, as well as a history of beetle scars and dated beetle-killed trees, provided sufficient evidence to suggest that a climate signal is not responsible for the growth releases we observed. For stands outside this region, however, we cannot entirely dismiss the possibility that some of the growth releases we detected were due to warmer and wetter than average growing conditions. Considerably more work may be required to extract climate signals from growth data for all of the stands we sampled. Still, synchronous growth release periods become more frequent among sampled stands over the last century. Historical reconstructions of climate indicate increasingly arid conditions over the last two centuries over much of southern British Columbia and Alberta (this study and Watson and Luckman 2001). As such, we would expect to see fewer increases in radial growth with time, unless a substantial canopy disturbance occurred. Thus, our working hypothesis remains that increases in the frequency of growth release periods among the stands we sampled are largely due to increasingly widespread beetle outbreaks.

This is consistent with recent aerial surveys indicating the range of beetle outbreaks is expanding further north and east to regions in which they were not able to persist previously.

One limitation to reconstructing the history of beetle outbreaks in this study is that tree-ring data came largely from stands that were dominated by lodgepole pine when sampled. Throughout much of British Columbia, lodgepole pine dominates early seral stands and are replaced by more shade tolerant and longer-lived conifer species within 150-200 years (e.g., Romme and Knight 1981; Campbell and Antos 2003). Thus, tree-ring chronologies from lodgepole pine are generally not much longer than 200 years. As a consequence, the sample size from which we can infer beetle outbreaks from tree-ring data becomes smaller further back in time, although releases from small host trees that were suppressed in the understory can compensate for this to some degree. In regions where a long history of low-intensity fires is thought to have maintained lodgepole pine on sites for at least two centuries (Romme and Knight 1981; Johnson and Fryer 1989), we might expect to find older lodgepole pine from which we could reconstruct beetle outbreaks. Even so, we did not find many old trees in the Cariboo-Chilcotin Plateau in central British Columbia, where lodgepole pine forests are thought to have long persisted in this region due to fire (Meidinger and Pojar 1991). It is possible that a long history of beetle outbreaks in this region has periodically removed the oldest and largest lodgepole pine. This seems a plausible explanation given that the lodgepole pine we sampled at Saskatchewan Crossing in Banff National Park were about 360 years old and apparently untouched by beetle outbreaks until recently. Other means of reconstructing beetle outbreaks similar to those used for reconstructing long histories of beetle outbreaks using macrofossils (Simard et al. 2002) should be considered.

4.2   Climate–beetle outbreak relationships

Climate changes have important implications for many biological processes, including for mountain pine beetle populations and outbreak dynamics. Changes in temperature and precipitation can have strong direct effects on insect survival, reproduction, phenology (i.e., timing of lifecycle stages), and dispersal, or indirect impacts by changing host physiology and interactions with natural enemies. It has been proposed that the more widespread beetle outbreaks we are observing currently are partly due to warming temperatures (Logan and Powell 2001; Carroll et al. 2004). We investigated relationships between outbreaks and climate by using historical instrumental weather data and tree-ring reconstructions of climate variables that would have an important effect on beetle development or host resistance to attack.

We first compared historical evidence of beetle outbreaks (i.e., documentary evidence and tree-ring growth release data) with historical instrumental weather data for the Cariboo-Chilcotin Plateau and Banff National Park. We found that beetle outbreaks of the 1930s/1940s and the 1970s/1980s in the Cariboo-Chilcotin Plateau and Banff National Park were preceded by drought. In Banff National Park, an unprecedented period of warm summers occurred when infestations of the 1970s/1980s developed. Our findings on beetle outbreaks and drought are consistent with a long history of observations that long periods of warm, dry weather typically precede insect outbreaks (Mattson and Haack 1987). In the case of mountain pine beetle, warmer temperatures increase reproductive success (Safranyik and Carroll 2006), and drought probably lowers host resistance by decreasing resin flow that normally prevents beetles from colonizing hosts.

Using the climate model ClimateBC we estimated annual, seasonal, and monthly climate conditions for all sampled stands (based on 1961-1990 climate normals obtained from interpolated weather station data). Stands at the current north and east edges of the beetle's geographic range (e.g., Prince George, Jasper and Banff National Parks) had the coldest annual temperatures (-0.69 to -2.2°C). No beetle outbreaks or minimal localized infestations occurred in these stands. Stands in the warmest and most arid regions (e.g., Kamloops and south of Williams Lake) had frequent beetle outbreaks. Model-generated climate data and beetle outbreak data (tree-ring evidence of outbreaks) by biogeoclimatic zone indicated a trend toward more frequent beetle

outbreaks in the warmest and driest regions of British Columbia (i.e., the IDF dk and dm zones where MAT = -1.8°C and 3.2°C, SHM = 49 and 83, respectively). Outbreaks of the 1970s/1980s tended to be less frequent in lodgepole pine stands of moister (e.g., ICH zone) and colder (e.g., SBS) regional climates and in higher elevation forests (e.g., ESSF zone). Our results comparing historical outbreak frequency obtained from tree-ring data to spatial variations in climate are consistent with what was expected based on current knowledge of beetle biology (Safranyik and Carroll 2006). Although we were able to distinguish trends, we found considerable variability in outbreak frequency among climatic zones and expect that local site conditions (e.g., slope aspect) and stand age are confounding factors.

Using the results of analyses of radial growth relationships and climate (i.e., PRECON analyses), we reconstructed the long-term climate in the Cariboo-Chilcotin Plateau (IDF biogeoclimatic zone), where outbreaks have likely occurred for centuries, and in Banff National Park, where outbreaks are considered to have occurred more recently. The models we developed to describe relationships between tree-ring width and climate in Banff National Park successfully predicted data set aside to test the models. We found that arid Junes were much more frequent during the 20th century than in the 19th century. We did not, however, find that October temperatures warmed significantly. Rather, they were warmest around the 1900s and again in the late 1970s and 1980s. The increasing likelihood of summer drought of the last two centuries, accompanied by warmer October temperatures in the 1970s/1980s, may partly explain why beetle outbreaks have not persisted in the park until recently. We expect that warmer spring temperatures will also have an important influence on beetle survivorship, but we were not able to reconstruct this from our tree-ring data. Tree-ring widths were significantly related to both spring (March) and fall (October) temperatures in the Cariboo-Chilcotin Plateau, but the models we developed to reconstruct temperature and summer aridity were not able to predict (with greater than 90% confidence) the measured data we set aside to test the models. Further work is required to explore other approaches to reconstructing climate in this region. Although we could not accurately predict monthly climate values, we did detect distinct differences in trends among Banff National Park and the Cariboo-Chilcotin Plateau. Reconstructed aridity indices for the Cariboo-Chilcotin Plateau indicate no significant change in summer aridity over the past two centuries, suggesting that this region has been quite dry for some time. Like October temperatures in Banff National Park, warmer than average March and October temperatures occurred periodically over the last two centuries and frequently coincided with shifts in the Pacific Decadal Oscillation. More work is needed to determine if apparent past oscillations in fall or spring temperatures occur within a larger, overall linear increase in temperatures. Although increasing drought may be making trees less resistant to beetle infestation in Banff National Park, in the Cariboo-Chilcotin Plateau where drought is persistent, warm spring and fall temperatures may have more of an influence on the occurrence of beetle outbreaks.

Future climate conditions were predicted for each of the stands from which we collected tree-ring data. The model predicted an increase in MAT of about 1°C from 1975 to the 2020s, from the 2020s to the 2050s, and from the 2050s to the 2080s. Model predictions indicated that the greatest increases in temperature would occur in the spring (February, March, and April). Cold-related mortality of beetles can also occur in the spring; warmer springs will provide more suitable conditions for beetles to complete their lifecycle and, therefore, for populations to increase. The current outbreaks in colder regions of northern British Columbia and in Alberta (areas where they have not occurred before, according to documentary evidence and tree-ring data) suggests that relatively small increases in temperature (probably spring temperatures) since the 1970s/1980s outbreak are causing an expansion in the range of beetle outbreaks. Tree-ring data indicated that outbreaks were somewhat less frequent among higher elevation stands (i.e., stands in the ESSF

and MS biogeoclimatic zones). Climate model predictions indicate similar increases in temperature in these high elevation stands (i.e., ~ 1°C). Thus, as with increasing northern and eastern expansion of suitable beetle climates, we expect outbreaks could become more frequent in higher elevation lodgepole pine stands, and even whitebark pine stands.

4.3   Mountain pine beetle outbreaks and fire history

More widespread mountain pine beetle outbreaks in western Canada may, at least in part, be caused by forest management activities (e.g., harvest regulation, fire suppression) that have increased the abundance of susceptible (i.e., mature) lodgepole pine forests over landscapes. We tested this hypothesis by examining relationships between the occurrence of beetle outbreaks and fire history. For selected areas, we looked at how the occurrence of fire had changed over time and described how the frequency of beetle outbreaks varied with fire regimes and time since the last major stand-replacing fire.

Fire scar data collected from the Cariboo-Chilcotin Plateau of central British Columbia indicated fires rarely occurred after 1920. This coincides with an increase in the extent of beetle outbreaks during the 1930s/s1940s and the 1970s/1980s in this region. Our finding is consistent with other studies showing that historical fire suppression and control policies are associated with more widespread insect outbreaks (McCullough et al. 1998).

Over a much larger spatial scale, we examined relationships between outbreaks and regional fire regimes. Although we found no significant difference in the frequency of beetle outbreak related to fire frequency, we did find that stands with a history of low-severity or mixed-severity fires had a greater risk of beetle outbreaks. This is probably because periodic low-severity fires maintain many mature trees on a site, making the stand continually susceptible to outbreaks. Stand-replacing fires, on the other hand, generate new even-aged lodgepole pine stands that are generally resistant to beetle outbreaks until they are 60 years old (Safranyik and Carroll 2006).

Using germination dates of lodgepole pine, we determined which of the 85 stands from which we collected tree-ring data grew from stand-replacing fires. Time-since-fire was calculated from peak lodgepole pine germination dates and stands were grouped into four time-since-fire categories: 0-50 years, 51-100 years, 101-150 years, and >150 years. We found that mountain pine beetle outbreaks were most frequent among stands that were 50-100 years old. This is consistent with the long-held observation that younger stands are less vulnerable to beetle outbreaks (Safranyik et al. 1975), probably because they are more resistant to the bluestain fungus, which usually interferes with resin production that prevents mass attacks on young trees. We found a pronounced decrease in the frequency of beetle outbreaks among stands 101-150 years old, but an increase again among stands >150 years old. It is possible that older trees are less able to support high beetle population because competition for brood space and food is higher within the thinner phloem of older trees. The increase in outbreak frequency among the oldest time-since-fire category (>150 years) is based on a small sample size ($n = 4$), making the results difficult to generalize.

5   Conclusions

Information about beetle outbreak dynamics (i.e., return-interval, intensity, and extent) will serve to better understand the function of mountain pine beetle in forest ecosystems. It is also a necessary component of landscape level models that predict the impact of outbreaks on timber supply. Development of tree growth responses to climate will provide tools to assess potential impacts of climate change on tree growth and beetle outbreaks. An understanding of beetle disturbance regimes and their interaction with fire will provide essential knowledge for the development of forest management strategies aimed at emulating natural disturbance regimes. This project will also permit better estimates of loss to beetle by measuring the rate of recovery and growth gains in the post-outbreak period, leading to better MAI estimates.

6   Acknowledgements

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Table A1. Characteristics of lodgepole pine growth releases for 85 stands sampled in British Columbia and Alberta. A release was defined as at least a 25% increase in growth compared to the previous 10 years (nrd = no release detected).

Stand	First year of master chronology	Growth release period	Duration of release (years)	Return interval between releases (years)	Mean magnitude of growth release
British Columbia:					
Kathleen Mountain 1	1907	1907-1910	4	--	1.50
		1936-1940	5	29	1.65
Kathleen Mountain 2	1792	1925-1937	13	--	1.57
		1973-1977	5	48	1.67
Kathleen Mountain 3	1882	nrd·	--	--	--
Castlegar	1943	nrd	--	--	--
Stem 1	1883	1885-1889	5	--	1.82
		1938-1945	8	53	1.61
Stem 2	1886	nrd	--	--	--
Moyie Lake	1887	1889-1897	9	--	1.43
		1910-1913	4	21	1.72
Angus Creek 1	1857	nrd	--	--	--
Angus Creek 2	1863	1941-1943	3	--	1.47
Laluwissin 1	1880	1897-1904	8	--	1.77
		1935-1943	9	38	1.84
Laluwissin 2	1882	1895-1904	10	--	1.60
Laluwissin 3	1866	1874-1879	6	--	1.33
Tunkwa Prov. Park	1881	1925-1940	16	--	2.51
		1977-1982	6	52	1.55
Correction Camp	1896	1927-1941	15	--	2.08
		1975-1981	7	48	1.57
Savona Prov. Park	1880	1934-1943	10	--	1.98
Kettle Valley 1	1901	nrd	--	--	--
Kettle Valley 2	1881	1936-1941	6	--	1.55
		1976-1984	9	40	1.74
Kettle Valley 3	1903	nrd	--	--	--
Manning Park 1	1860	1933-1946	14	--	1.64
		1976-1978	3	43	1.34
Manning Park 2	1845	1936-1949	14	--	1.73
Manning Park 3	1877	1937-1941	5	--	1.49
		1955-1967	13	18	1.81
Manning Park 4	1869	1963-1967	5	--	1.74
Manning Park 5	1863	1933-1946	14	--	1.71
		1976-1978	3	43	1.54
Doig Road	1913	1960-1962	3	--	1.64
Tweedsmuir Park 2	1912	nrd	--	--	--
Tweedsmuir Park 3	1944	nrd	--	--	--
Tweedsmuir Park 4	1866	1936-1938	3	--	1.52
Tweedsmuir Park 5	1943	nrd	--	--	--

Table A1 (cont.)

Tweedsmuir Park 6	1944	nrd	--	--	--
Tweedsmuir Park 7	1863	nrd	--	--	--
Tweedsmuir Park 8	1934	nrd	--	--	--
Tweedsmuir Park 9	1927	nrd	--	--	--
Bull Mountain	1861	1871-1874	4	--	1.42
		1930-1936	7	59	1.49
		1955-1961	7	25	1.83
		1974-1981	8	19	2.01
Cariboo-Chilcotin 101	1855	1935-1940	6	--	1.51
		1974-1978	5	39	1.47
Cariboo-Chilcotin 102	1889	1889-1895	7	--	1.58
		1924-1928	5	35	1.54
		1939-1942	4	15	1.52
		1975-1978	4	36	1.80
Cariboo-Chilcotin 103	1826	1873-1879	7	--	1.86
		1939-1942	4	66	1.39
		1983-1991	9	44	2.40
Cariboo-Chilcotin 104	1824	1848-1858	11	--	1.88
		1873-1882	10	25	1.80
		1937-1943	7	64	1.50
		1972-1981	10	35	1.58
Cariboo-Chilcotin 105	1867	1934-1943	10	--	1.58
Cariboo-Chilcotin 106	1843	1937-1942	6	--	1.56
Cariboo-Chilcotin 107	1886	1913-1920	8	--	1.71
		1977-1983	7	64	1.60
Cariboo-Chilcotin 108	1868	1891-1899	9	--	1.60
		1975-1979	5	84	1.68
Cariboo-Chilcotin 109	1799	1851-1853	3	--	1.37
		1857-1862	6	6	1.57
		1875-1879	5	18	1.41
		1927-1941	15	52	1.66
		1976-1979	4	49	1.67
Cariboo-Chilcotin 110	1803	1859-1868	10	--	1.62
		1875-1889	15	16	1.77
		1926-1940	15	51	1.65
		1976-1978	3	50	1.59
Cariboo-Chilcotin 111	1859	1876-1878	3	--	1.42
		1934-1940	7	58	1.41
		1975-1979	5	41	1.72
Cariboo-Chilcotin 112	1884	1938-1940	3	--	1.51
		1964-1967	4	26	1.44
		1973-1978	6	9	1.56
Cariboo-Chilcotin 113	1794	1923-1933	11	--	1.59
		1958-1966	9	35	1.80
Cariboo-Chilcotin 114	1869	1928-1941	14	--	1.44
		1975-1978	4	47	1.60
Cariboo-Chilcotin 115	1796	1840-1843	4	--	1.86
		1864-1879	16	24	1.46
		1899-1902	4	35	1.78
		1973-1978	6	74	1.75

Table A1 (cont.)

Cariboo-Chilcotin 116	1874	1937-1942	6	--	1.51
		1972-1988	17	35	1.74
Cariboo-Chilcotin 117	1886	1818-1820	3	--	1.26
		1870-1877	8	52	1.97
		1937-1941	5	67	1.54
		1974-1979	6	37	1.80
Cariboo-Chilcotin 118	1849	1897-1899	3	--	1.67
		1935-1939	5	38	1.50
		1975-1991	17	40	1.76
Cariboo-Chilcotin 119	1861	1936-1938	3	--	1.46
		1978-1981	4	42	1.66
Cariboo-Chilcotin 120	1799	1801-1807	7	--	1.60
		1891-1893	3	90	1.37
		1937-1943	7	46	1.49
Cariboo-Chilcotin 121	1896	1897-1901	5	--	1.52
		1977-1986	10	80	1.57
Cariboo-Chilcotin 122	1889	nrd	--	--	--
Cariboo-Chilcotin 123	1885	1937-1939	3	--	1.39
		1976-1979	4	39	1.45
Cariboo-Chilcotin 124	1914	1960-1964	5	--	1.55
		1988-1990	3	28	1.40
Cariboo-Chilcotin 125	1895	1933-1940	8	--	2.19
		1975-1982	8	42	1.61
Cariboo-Chilcotin 126	1824	1860-1864	5	--	1.81
		1892-1899	8	32	1.98
		1934-1942	9	42	1.58
		1959-1963	5	25	1.49
		1975-1981	7	16	1.59
Cariboo-Chilcotin 128	1925	1930-1939	10	--	1.68
		1973-1987	15	43	2.25
Cariboo-Chilcotin 129	1880	1890-1894	5	--	1.68
		1934-1942	9	44	1.81
		1977-1991	15	43	1.76
Cariboo-Chilcotin 130	1894	1933-1942	10	--	1.99
		1975-1991	17	42	1.94
Cariboo-Chilcotin 163	1886	1934-1943	10	--	1.77
Cariboo-Chilcotin 359	1908	1935-1942	8	--	1.71
		1976-1978	3	41	1.60
Whiteswan Prov. Park	1889	1895-1900	6	--	1.17
		1927-1931	5	32	2.04
		1942-1947	6	15	1.99
		1981-1986	6	39	1.64
Kamloops 302	1881	1935-1942	8	--	1.45
		1960-1964	5	25	1.57
		1975-1991	17	15	1.69
Parson	1940	1944-1946	3	--	1.33
Cranbrook	1920	nrd	--	--	--
Hall Lake	1871	1897-1901	5	--	1.17
		1976-1983	8	79	1.49

Table A1 (cont.)

Revelstoke 1	1862	nrd	--	--	--
Revelstoke 2	1873	1933-1940	8	--	2.04
Golden 3	1885	1976-1981	6	--	1.46
Golden 4	1907	1963-1981	19	--	1.77
Canal Flats 12	1863	1947-1953	7	--	1.40
		1975-1989	15	28	1.77
Canal Flats 13	1889	1895-1927	33	--	1.94
		1974-1984	11	79	1.82
Okanagan Falls 14	1811	1898-1901	4	--	1.36
		1938-1942	5	40	1.41
		1961-1964	4	23	1.39
Okanagan Falls 15	1836	1889-1908	20	--	1.96
		1940-1942	3	51	1.36
Okanagan Falls 16	1887	1923-1929	7	--	1.61
		1938-1949	12	15	1.54
Kootenay National Park	1894	1927-1929	3	--	1.36
		1935-1946	12	8	1.42
		1986-1994	9	51	1.69
Prince George	1862	1931-1933	3	--	1.59
		1974-1979	6	43	2.09
Alberta:					
Banff National Park 5	1837	1955-1963	9	--	1.82
		1977-1984	8	22	1.60
Banff National Park 8	1902	nrd	--	--	--
Blairemore 9	1912	1918-1920	3	--	1.52
Blairemore 10	1887	1897-1901	5	--	1.45
		1955-1962	8	58	1.43
		1978-1988	11	23	2.39
Blairemore 11	1880	1879-1898	20	--	1.62
		1938-1947	10	59	2.16
Jasper National Park 1	1857	1892-1911	20	--	2.08
Jasper National Park 2	1874	1908-1911	4	--	1.76
Jasper National Park 3	1634	1847-1849	3	--	1.36
		1876-1880	5	29	1.41
		1899-1904	6	23	1.51
		1935-1943	9	36	1.60
		1963-1969	7	28	1.52
		1974-1986	13	11	1.53
Waterton National Park	1890	1895-1897	3	--	1.30
		1986-1988	3	91	1.91
Mean			**7.78**	**40.26**	**1.65**

Table A2. Characteristics of non-host growth releases for 47 stands sampled in British Columbia and Alberta

Note: (AF = subalpine fir, DF = Douglas-fir, HW = western hemlock, LW = western larch, SE = Engelmann spruce, SW = white spruce) (nrd = no release detected).

Stand	Species	First year of master chronology	Growth release period	Duration of release (years)	Return interval between releases (years)	Mean magnitude of growth release
British Columbia:						
Kathleen Mountain 1	SE	1933	1933-1944	12	--	1.61
	SE		1955-1958	4	22	1.79
Kathleen Mountain 2	SE	1857	1858-1861	4	--	1.34
	SE		1871-1885	15	13	1.45
	SE		1936-1946	11	65	1.39
Kathleen Mountain 3	SE	1878	1884-1888	5	--	1.47
Castlegar	SE	1943	nrd·	--	--	--
Stem 1	SE	1859	1865-1883	19	--	1.48
	SE		1940-1949	10	75	1.54
Stem 2	SE	1800	1872-1884	13	--	1.97
Moyie Lake	SE	1897	nrd	--	--	--
Angus Creek 1	SE	1879	1981-1983	3	--	1.37
Laluwissin 1	DF	1819	1872-1880	9	--	2.02
	DF		1898-1905	8	26	1.62
	DF		1933-1950	18	35	1.71
Laluwissin 2	DF	1758	1848-1855	8	--	1.40
	DF		1874-1877	4	26	1.45
	DF		1893-1900	8	19	1.50
	DF		1933-1943	11	40	1.46
Laluwissin 3	SE	1879	nrd	--	--	--
Tunkwa Provincial Park/Correction Camp	SE	1879	1928-1940	13	--	1.86
Savona Provincial Park	DF	1648	1650-1658	9	--	0.95
	DF		1686-1694	9	36	1.44
	DF		1765-1772	8	79	1.30
	DF		1776-1785	10	11	1.80
	DF		1797-1806	10	21	1.90
	DF		1867-1878	12	70	1.87
	DF		1891-1899	9	24	1.74
	DF		1933-1941	9	42	1.58
Kettle Valley 1	DF	1912	1989-1993	5	--	1.47
Kettle Valley 2	SE	1882	1958-1966	9	--	3.30
Kettle Valley 3	SE	1909	1976-1978	3	--	1.41
Manning Park 1	DF	1894	1977-1984	8	--	1.74
	SE	1903	1904-1913	10	--	1.48
	SE		1933-1947	15	29	2.02
	SE		1977-1981	5	44	1.33
Manning Park 2	DF	1857	1933-1946	14	--	1.59
	DF		1977-1983	7	44	1.69
Manning Park 3	DF	1904	1957-1965	9	--	1.83
	DF		1976-1984	9	19	1.35

Table A2 (cont.)

Manning Park 4	SE	1896	1896-1900	5	--	1.33
	SE		1906-1917	12	10	1.60
	SE		1937-1950	14	31	1.43
Manning Park 5	AF	1948	1976-1983	8	--	1.37
	DF	1879	1933-1938	6	--	1.50
Tweedsmuir Park 2	SW	1923	nrd	--	--	--
Tweedsmuir Park 5-8	SW	1855	nrd	--	--	--
Bull Mountain	DF	1762	1777-1780	4	--	1.37
	DF		1800-1815	16	23	1.83
	DF		1926-1933	8	126	1.44
	DF		1974-1981	8	48	1.68
Whiteswan Provincial Park	DF	1889	1940-1942	3	--	1.53
	DF		1958-1962	5	18	1.43
	DF		1978-1983	6	20	1.70
Kamloops 305	DF	1883	1926-1928	3	--	1.44
	DF		1976-1984	9	50	1.65
Cranbrook	WL	1929	1959-1963	5	--	1.39
	WL		1991-1993	3	32	1.47
Revelstoke 1	DF	1866	1958-1961	4	--	1.36
Revelstoke 2	HW	1883	1893-1900	8	--	1.65
	HW		1934-1945	12	41	1.59
Golden 3	DF	1893	1900-1907	8	--	1.41
Golden 4	DF	1907	1972-1981	10	--	1.63
Canal Flats 12	DF	1902	1902-1907	6	--	1.27
	DF		1911-1927	17	9	1.26
	DF		1950-1963	14	39	1.41
Canal Flats 13	DF	1928	1973-1981	9	--	1.87
Okanagan Falls 15	SE	1811	1877-1882	6	--	1.47
	SE		1891-1913	23	14	2.41
	SE		1982-1986	5	91	1.41
Alberta:						
Banff National Park 5	SE	1855	1885-1898	14	--	1.44
	SE		1919-1927	9	34	1.47
	SE		1943-1945	3	24	1.39
Banff National Park 6	SE	1903	1913-1920	8	--	1.53
Blairemore 9	SE	1928	nrd	--	--	--
Blairemore 10	SE	1937	1962-1969	8	--	1.54
	SE		1974-1990	17	12	1.56
Blairemore 11	SE	1868	1938-1946	9	--	1.83
Waterton National Park	DF	1936	1955-1957	3	--	1.48
	DF		1978-1986	9	23	1.59
	SW	1893	1923-1929	7	--	1.53
	SW		1939-1941	3	16	1.49
	SW		1976-1991	16	37	1.69
Mean				**8.94**	**35.95**	**1.58**

Table A3. Frequency of mountain pine beetle outbreaks (based on growth release data) by biogeoclimatic zone.

Note: AB = Alberta, ESSF = Engelmann Spruce-Subalpine Fir zone (dc, dm, mw), ICH = Interior Cedar-Hemlock zone (subzones: dm, mk, mw, vk, wk), IDF = Interior Douglas-fir (dk, dm), MS = Montane Spruce (dk, dm, xk, xv), SBPS = Sub-Boreal Pine – Spruce (xc), SBS = Sub-Boreal Spruce (dk, dw, mc). Lower case codes in brackets refer to regional climates within biogeoclimatic zones.

Stand	# of trees	1940s outbreak period		1980s outbreak period	
		% trees released	Beetle outbreak	% trees released	Beetle outbreak
AB:					
BAN05	20	70.0	Yes	30.0	Yes
BAN08	20	0.0	No	5.0	No
BLR09	23	0.0	No	13.0	No
BLR10	14	35.7	Yes	22.4	No
BLR11	18	77.8	Yes	5.6	No
JASP	11	18.2	No	18.2	No
WAT	19	10.5	No	38.0	Yes
JWG	15	6.7	No	13.3	No
SASKX	16	31.3	Yes	31.3	Yes
Outbreak frequency			**42.9%**		**28.6%**
ESSF dc,dm,mw:					
OK16	16	50.0	Yes	12.5	No
ANG1	26	11.5	No	26.9	No
ANG2	27	25.9	No	14.8	No
PARS	10	0.0	No	0.0	No
MAN1	12	41.7	Yes	0.0	No
MAN2	19	57.9	Yes	31.6	Yes
MAN3	9	77.8	Yes	22.2	No
MAN4	14	14.3	No	14.3	No
MAN5	17	58.8	Yes	11.8	No
Outbreak frequency			**55.6%**		**11.1%**
ICH dm,mk,mw,vk,wk:					
MOY	28	0.0	No	3.6	No
GOLD03	15	13.3	No	20.0	No
KET1	28	0.0	No	7.1	No
KET2	28	28.6	No	42.9	Yes
KET3	27	22.2	No	18.5	No
CAST	29	0.0	No	6.9	No
CC107	20	5.0	No	15.0	No
GOLD04	18	0.0	No	50.0	Yes
REV01	15	26.7	No	6.7	No
REV02	16	43.8	Yes	18.8	No
Outbreak frequency			**10.0%**		**20.0%**
IDF dk,dm:					
BULL	40	42.5	Yes	57.5	Yes
CC102	30	33.3	Yes	46.7	Yes
CC103	43	11.6	No	25.6	No
CC104	29	20.7	No	27.6	No
CC105	15	40.0	Yes	20.0	No
CC106	26	26.9	No	11.5	No
CC109	12	41.7	Yes	25.0	No
CC116	32	25.0	No	40.6	Yes
CC117	26	15.4	No	30.8	Yes
CC121	34	5.9	No	5.9	No
CC126	30	26.7	No	23.3	No
CC128	23	13.0	No	43.5	Yes

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CC163	7	42.9	Yes	14.3	No
CC359	15	26.7	No	26.7	No
CORR	30	86.7	Yes	23.3	No
K302	8	37.5	Yes	75.0	Yes
LAL1	29	44.8	Yes	3.4	No
LAL2	22	22.7	No	13.6	No
SAVO	28	67.9	Yes	7.1	No
ST2B	24	45.8	Yes	0.0	No
TUNK	29	82.8	Yes	31.0	Yes
HALL	19	10.5	No	26.3	No
Outbreak frequency			**50.0%**		**31.8%**
MS dk,dm,xk,xv:					
CAN12	8	25.0	No	25.0	No
CAN13	18	11.1	No	55.6	Yes
WHIT	9	44.4	Yes	33.3	Yes
KOOT	10	60.0	Yes	60.0	Yes
KATHA	29	24.1	No	13.8	No
OK14	21	14.3	No	14.3	No
OK15	12	8.3	No	84.0	Yes
KATHC	20	5.0	No	5.0	No
KATHB	22	27.3	No	27.3	No
LAL3	26	7.7	No	0.0	No
ST2C	27	3.7	No	3.7	No
CC101	27	14.8	No	7.4	No
Outbreak frequency			**18.2%**		**27.3%**
SBPS xc:					
CC108	30	3.3	No	33.3	Yes
CC110	16	56.3	Yes	6.3	No
CC111	41	9.8	No	31.7	Yes
CC112	28	25.0	No	21.4	No
CC113	13	46.2	Yes	23.1	No
CC114	27	42.3	Yes	23.1	No
CC115	19	21.1	No	0.0	No
CC118	25	36.0	Yes	40.0	Yes
CC119	26	7.7	No	11.5	No
CC120	11	9.1	No	0.0	No
CC122	34	8.8	No	8.8	No
CC123	25	4.0	No	12.0	No
CC124	15	13.3	No	6.7	No
CC125	25	48.0	Yes	20.0	No
CC129	19	42.1	Yes	47.4	Yes
CC130	24	45.8	Yes	33.3	Yes
Outbreak frequency			**43.8%**		**31.3%**
SBS dk,dw,mc:					
TWD2	14	14.3	No	7.1	No
TWD3	14	0.0	No	0.0	No
TWD4	14	35.7	Yes	7.1	No
TWD5	9	0.0	No	0.0	No
TWD6	10	0.0	No	0.0	No
TWD7	14	7.1	No	0.0	No
TWD8	13	0.0	No	0.0	No
TWD9	15	0.0	No	6.7	No
PG	15	20.0	No	33.3	Yes
DOIG	18	11.1	No	27.8	No
Outbreak frequency			**10.0%**		**10.0%**

Table A4. Pearson correlation coefficients (*r*) indicating relationships between:

i) the Pacific Decadal Oscillation (PDO) and tree-ring chronologies (standard and residual), and
ii) PDO and climate. Data are presented for the Cariboo-Chilcotin Plateau, British Columbia and Banff National Park, Alberta. Significant correlations (*p* < 0.05) are indicated in **bold** (PL = lodgepole pine, DF = Douglas-fir).

	Cariboo-Chilcotin Plateau	Banff National Park
Standard chronology (PL)	—	**0.379**
Residual chronology (PL).	—	0.107
Standard chronology (DF)	—	-0.091
Residual chronology (DF).	—	-0.020
Standard chronology (PL)	0.111	—
Residual chronology (PL).	0.097	—
Standard chronology (DF)	-0.189	—
Residual chronology (DF).	-0.194	—
Mean January temp. (°C)	0.215	**0.276**
Mean February temp.	0.014	0.123
Mean March temp.	**0.395**	**0.262**
Mean April temp.	**0.427**	**0.247**
Mean May temp.	**0.251**	0.185
Mean June temp.	0.136	0.026
Mean July temp.	0.118	0.068
Mean August temp.	-0.014	-0.131
Mean September temp.	-0.143	-0.132
Mean October temp.	**0.237**	0.136
Mean November temp.	0.100	0.014
Mean December temp.	0.189	**0.243**
Mean annual temp.	**0.380**	**0.371**
Mean summer temp.	0.191	0.050
Mean January ppt. (mm)	-0.121	**-0.278**
Mean February ppt.	-0.052	**-0.310**
Mean March ppt.	-0.125	-0.051
Mean April ppt.	-0.083	-0.088
Mean May ppt.	0.007	0.107
Mean June ppt.	-0.004	0.170
Mean July ppt.	-0.014	-0.036
Mean August ppt.	0.052	0.080
Mean September ppt.	**0.322**	0.176
Mean October ppt.	-0.163	-0.156
Mean November ppt.	-0.197	-0.004
Mean December ppt.	-0.191	**-0.232**
Total annual ppt.	-0.151	-0.130
Total summer ppt.	0.024	0.145
Aridity Index	0.000	-0.043

Table A5. Frequency of mountain pine beetle outbreaks by fire frequency class. Data indicating the occurrence of beetle outbreaks were pooled for the 1940s and 1980s outbreak periods.

Fire frequency class (yrs)	N	Frequency of beetle outbreaks (%)
0-35	76	36
35-100	92	26
100-200	6	33

N = number of stands sampled, multiplied by 2, as outbreak data from the 1940s and 1980s were pooled.

Table A6. Frequency of mountain pine beetle outbreaks by fire severity class. Data indicating the occurrence of beetle outbreaks were pooled for the 1940s and 1980s outbreak periods.

Fire severity class	N	Frequency of beetle outbreaks (%)
low severity	36	36
mixed severity	94	33
stand-replacing	46	24

N = number of stands sampled, multiplied by 2, as outbreak data from the 1940s and 1980s were pooled.

Table A7. Frequency of mountain pine beetle outbreaks as a function of time since last stand-replacing fire. Data indicating the occurrence of beetle outbreaks were pooled for the 1940s and 1980s outbreak periods.

| Time since fire (yrs)	N	Frequency of beetle outbreaks (%)
0-50	36	14
51-100	64	36
101-150	22	24
>150	4	50

N = number of stands sampled, multiplied by 2, as outbreak data from the 1940s and 1980s were pooled.

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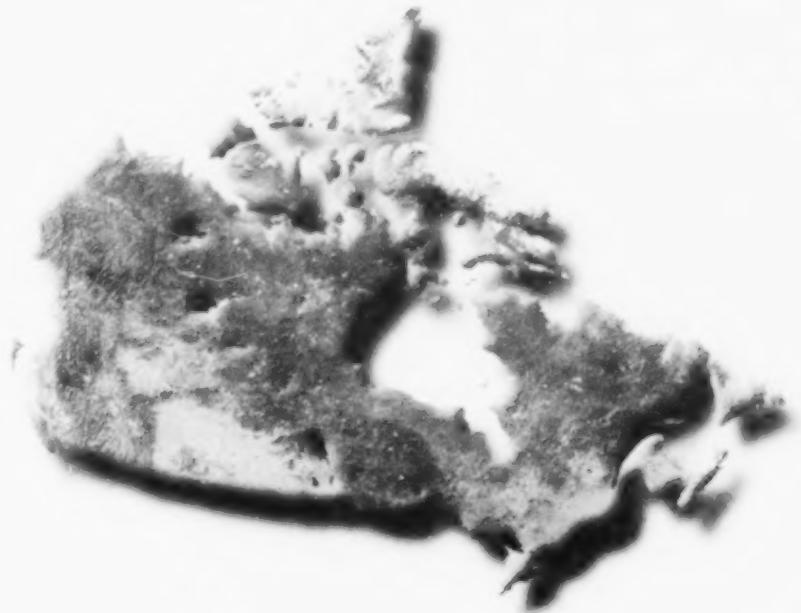
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